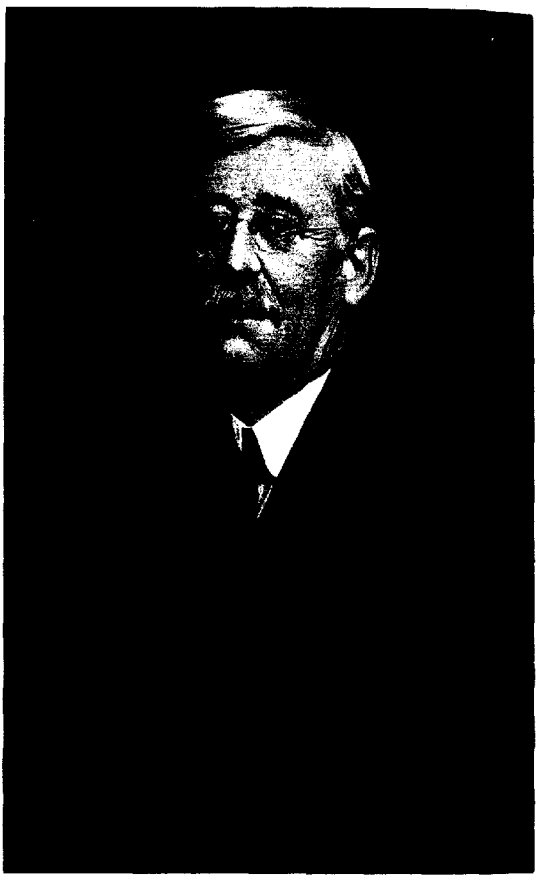

Yours sincerely
Byron D. Halsted

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BYRON DAVID HALSTED[1]

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F. L. STEVENS, L. H. PAMMEL, AND MEL T. COOK

"I loved Byron for the genuineness of his religious faith, for the simplicity and beauty of his relationship to his fellows, for his ardent desire for service to the world and catholic tolerant spirit exercised toward those who differed from him in faith and thought." This appreciation of Dr. Halsted by an intimate friend will find response in the hearts of all who knew him. However brilliant the achievements of the individual from the world viewpoint, whether in finance, art, literature, or science, it is to the personality, the characteristics, traits, inclinations, and moralities, that we turn in making the ultimate estimate of the man. Dr. Halsted's genial nature, generosity, patriotism, and broad interest in art, music, literature, and athletics, as well as his scientific attainments, are the attributes that claim our homage.

He was one of the few of America's eminent pioneers in plant pathology, the first graduate student to take work under Dr. W. G. Farlow, the first to take the doctorate in cryptogamic botany at Harvard. He taught plant pathology at Ames when the subject was in its infancy in America, and there also he began a series of publications on plant pathology. Indefatigable and full of enthusiasm as a worker and keen as an investigator, a bibliography of his titles would number approximately four hundred, with contributions chiefly to plant pathology and plant breeding.

Dr. Halsted entered Michigan Agricultural College in 1867 and was graduated in 1871. He entered Harvard University in 1874 and received the degree of Doctor of Science in 1878 with a thesis on the "Classification and Description of the American Species of Characeae." He was managing editor of the *American Agriculturist* for five years, then went to the chair of botany of the Iowa Agricultural College, which position he held from 1885 to 1889, when he was elected to the professorship of botany at Rutgers College and the position of botanist of the New Jersey Agricultural College Experiment Station. In both institutions he endeared himself to students and faculty and laid broad, enduring foundations for botanical departments.

[1] Prepared at the request of the council of the Botanical Society of America.

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Many students owe their later successes in life and their contributions to the world's welfare to inspiration and ambition derived through contact with Dr. Halsted in these two colleges.

His interest centered primarily in plant pathology, and pioneer work was carried on regarding many fruit and truck crop diseases. He also gave special attention to the diseases of ornamental plants, a field in which his work probably overshadows that of all other contributors. While in New Jersey failing eyesight and health forbade further microscopic work and his activities were turned to field work in plant breeding.

Dr. Halsted was a member of Phi Beta Kappa. He also won the silver medal of the Massachusetts Horticultural Society and was a fellow of the American Association for the Advancement of Science. He served in an official capacity many of the leading national scientific societies of the country. He was elected president of the New Jersey Microscopical Society, second vice-president of the Iowa Academy of Science in 1888–1889, secretary of Section F of the American Association for the Advancement of Science in 1892, secretary of the Society for the Promotion of Agricultural Science in 1892, and its president from 1897 to 1899, and was president of the Botanical Society of America in 1900–1901. He was affiliated with other national societies—the Society for Plant Morphology and Physiology, the Society of Horticultural Science, the American Society of Naturalists, and was associate editor of the *Bulletin of the Torrey Botanical Club* (1890–1893) and a contributor to the *Systematic Flora of North America*.

Dr. Halsted was born at Venice, New York, of Quaker parentage June 7, 1852; was thrice married and leaves three children. He died at New Brunswick, New Jersey, the scene of his activities of nearly thirty years, on August 28, 1918.

PUBLICATIONS

The following is a list, as nearly complete as possible, of the scientific publications of Dr. Halsted, not including numerous abstracts and reviews of the work of other writers.

1877

Reproduction in fresh-water algae. Amer. Nat. **11**: 513–524.

1878

Notes upon vernation. Proc. Boston Soc. Nat. Hist. **19**: 215, 216.

1881

Classification and description of the American species of Characeae. Proc. Boston Soc. Nat. Hist. **20**: 169–190.

Barn plans and outbuildings. 235 pp. New York.

1883

Agricultural education for the young. Proc. Soc. Prom. Agr. Sci., 2d Ann. Meeting (1881): 54–56.

Notes on sassafras-leaves. Science **2**: 491–493.

A strange sassafras-leaf. Science **2**: 684, 685.

A combination walnut. Science **2**: 761, 762.

1884

Little things of great importance. Home Science. May, 1884, pp. 18–23.
Retrograde metamorphosis of a strawberry-flower. Science 3: 302.
Conditions of growth of the wheat-rust. Science 3: 457, 458.
Mildew and grape rot. Proc. N. J. State Hort. Soc., 9th Ann. Meeting (1884): 74–76.

1885

A potato disease. Proc. Soc. Prom. Agr. Sci., 5th Ann. Meeting (1884): 42–44.

1886

A new Iowa Aecidium. Journ. Mycol. 2: 52.
Gymnosporangium macropus on *Pirus coronaria*. Bot. Gaz. 11: 190, 191.
An interesting Peronospora. Bot. Gaz. 11: 272.
A pleasing experiment in laboratory practice. Bot. Gaz. 11: 339, 340.
Strange pollen-tubes of Lobelia. Amer. Nat. 20: 644, 645.

1887

Pollen-tubes of Lobelia. Amer. Nat. 21: 75, 76.
Bulletin of the Iowa Agricultural College, from the Botanical Department. 66 pp.
A plant heliostat. Bot. Gaz. 12: 82, 83.
"Crazy" pollen of the bell-wort. Bot. Gaz. 12: 139, 140.
Dry weather foliage of the compass plant. Bot. Gaz. 12: 161, 162.
Three nuclei in pollen grains. Bot. Gaz. 12: 285–288.
A new Uromyces. Journ. Mycol. 3: 138.
Dioecism in *Anemone acutiloba*, Lawson. Bull. Torrey Club 14: 119–121.
Germination of cucumber seed. Gard. Chron., 3d ser. 2: 466.
A hint as to nitrogen appropriation in clovers. Proc. Soc. Prom. Agr. Sci., 8th Ann. Meeting (1887): 41–44.
The peg in germinating cucurbitaceous plants. Proc. Soc. Prom. Agr. Sci., 8th Ann. Meeting (1887): 45–48.
The powdery mildew of the gooseberry. *Sphaerotheca mors-uvae*, B. and C. Rept. U. S. Comm. Agr. 1887: 373–380.

1888

Bulletin from the Botanical Department of the State Agricultural College, Ames, Iowa. 118 pp.
(With J. B. Ellis) New Iowa fungi. Journ. Mycol. 4: 7, 8.
Iowa Peronosporeae and a dry season. Bot. Gaz. 13: 52–59.
Pollen germination and pollen measurement (Abstr.). Bot. Gaz. 13: 238.
Trigger-hairs of the thistle flower. Bull. Torrey Club 15: 82–84.
Abnormal ash leaves. Bull. Torrey Club 15: 212, 213.
Fertilization of flowers. Proc. N. J. State Hort. Soc., 13th Ann. Meeting (1887): 101–108.
Apple rusts. Rept. U. S. Comm. Agr. 1888: 370–381.
Potato flowers and fruit. Proc. Soc. Prom. Agr. Sci., 9th Ann. Meeting (1888): 33, 34.
The tomato flower and fruit. Proc. Soc. Prom. Agr. Sci., 9th Ann. Meeting (1888): 35, 36.

1889

Peronosporeae and rain-fall. Journ. Mycol. 5: 6–11.
An interesting Uromyces. Journ. Mycol. 5: 11.
Notes upon *Sphaerotheca phytoptophila*, Kell. and Swingle. Journ. Mycol. 5: 85, 86.
Another Sphaerotheca upon Phytoptus distortions. Journ. Mycol. 5: 134.
Some notes upon economic Peronosporeae for 1889 in New Jersey. Journ. Mycol. 5: 201–203.
An investigation of apple twigs. Iowa Agr. Exp. Sta. Bull. 4: 104–132.

Pollen germination and pollen measurements (Abstr.). Proc. Amer. Assn. Adv. Sci. [illegible]: 288.
Our worst weeds. Bot. Gaz. **14**: 69–71.
A modification of the versatile anther. Bot. Gaz. **14**: 107, 108.
Pollen mother-cells. Bot. Gaz. **14**: 109.
Dicentra stigmas and stamens. Bot. Gaz. **14**: 129, 130.
Sensitive stamens in Compositae. Bot. Gaz. **14**: 151, 152.
Peronospora upon cucumbers. Bot. Gaz. **14**: 152, 153.
Observations upon barberry flowers. Bot. Gaz. **14**: 201.
Notes upon Lithospermum. Bot. Gaz. **14**: 202, 203.
Pickerel weed pollen. Bot. Gaz. **14**: 255–257.
Notes upon stamens of Solanaceae (Abstr.). Bot. Gaz. **14**: 260.
Reserve food substances in twigs (Abstr.). Bot. Gaz. **14**: 260.
The station botanists at Washington. Bot. Gaz. **14**: 305–309.
The germination of pollen. Bull. Torrey Club **16**: 130, 131.
Observations upon pollen measurements. Bull. Torrey Club **16**: 135, 136.
What are the worst weeds of New Jersey? N. J. Agr. Coll. Exp. Sta. Bull. 52. 15 pp.
Some fungus diseases of the cranberry. N. J. Agr. Coll. Exp. Sta. Bull. 64. 40 pp.
Pollen versus rain. Proposed experiments illustrating the influences of rainfall at blooming time upon subsequent fruitfulness. N. J. Agr. Coll. Exp. Sta. Spec. Bull. C. 4 pp.
The doubling of flowers. Proc. N. J. State Hort. Soc., 14th Ann. Meeting (1888): 74–84.
The cranberry gall fungus. Proc. Soc. Prom. Agr. Sci., 10th Ann. Meeting (1889): 39–43.
Our worst weeds: A scale of points. Proc. Soc. Prom. Agr. Sci., 10th Ann. Meeting (1889): 43–49.
The potato rot. N. J. Agr. Coll. Exp. Sta. Spec. Bull. G. 4 pp.
The cranberry scald. N. J. Agr. Coll. Exp. Sta. Spec. Bull. H. 3 pp.
The sweet potato rot. N. J. Agr. Coll. Exp. Sta. Spec. Bull. J. 3 pp.

1890

Treatment of cranberry scald and cranberry gall-fungus. Journ. Mycol. **6**: 18, 19.
(With J. B. Ellis) New fungi. Journ. Mycol. **6**: 33–35.
Once more about the weeds. Bot. Gaz. **15**: 23, 24.
Notes upon stamens of Solanaceae. Bot. Gaz. **15**: 103–106.
Peronospora rubi Rabenh. in America. Bot. Gaz. **15**: 179.
Collections of weeds. Bot. Gaz. **15**: 312.
Notes upon Peronosporeae for 1890. Bot. Gaz. **15**: 320–324.
Station botanists at Champaign. Bot. Gaz. **15**: 334–339.
Clipping currant clusters. Garden and Forest **3**: 19.
Worms in violet roots. Garden and Forest **3**: 69.
Hollyhock diseases. Garden and Forest **3**: 158.
Why not legislate against the black knot? Garden and Forest **3**: 194.
Anthracnose or blight of the oak. Garden and Forest **3**: 295, 296.
Legislation against fungous diseases in New Jersey. Garden and Forest **3**: 307, 308.
Nematodes and the oat crop. Garden and Forest **3**: 319, 320.
Anthracnose on the maple. Garden and Forest **3**: 325.
The egg-plant blight. Garden and Forest **3**: 457.
Botanical work at the stations. Garden and Forest **3**: 463, 464.
The celery blight. Garden and Forest **3**: 481.
Effect of forest-management on orchards. Garden and Forest **3**: 487, 488.
Nematodes in the chrysanthemum. Garden and Forest **3**: 499, 500.
Spraying against pear blight. Garden and Forest **3**: 505.
A dangerous enemy to the radish. Garden and Forest **3**: 541, 542.
The rot among late potatoes. Garden and Forest **3**: 551, 552.

Nematodes again. Garden and Forest 3: 565.
The root rot of salsify. Garden and Forest 3: 576.
The cranberry scald. Garden and Forest 3: 583, 584.
A new white smut. Bull. Torrey Club 17: 95–97.
Notes upon Ailanthus. Bull. Torrey Club 17: 102, 103.
Witches' huckleberries. Bull. Torrey Club 17: 104, 105.
Notes upon Zygodesmus and its new species. Bull. Torrey Club 17: 151, 152.
A possible natural hybrid. Bull. Torrey Club 17: 176, 177.
Reserve food-materials in buds and surrounding parts. Mem. Torrey Club 2: 1–26.
Some reasons for varieties not soon wearing out. Amer. Nat. 24: 577–581.
Report of the botanist. Rept. N. J. Agr. Exp. Stations (1889): 221–239.
Fungi injurious to horticulture. Proc. N. J. State Hort. Soc., 15th Ann. Meeting (1889): 149–162.
The rots of the sweet potatoes. Proc. Soc. Prom. Agr. Sci., 11th Ann. Meeting (1890): 27, 28.
Reserve food substances in twigs (Abstr.). Proc. Amer. Assn. Adv. Sci. (1889): 281, 282.
Some fungous diseases of the spinach. N. J. Agr. Coll. Exp. Sta. Bull. 70. 15 pp.
Some fungous diseases of the sweet potato. N. J. Agr. Coll. Exp. Sta. Bull. 76. 32 pp.
Observations upon the peach for 1890. N. J. Agr. Coll. Exp. Sta. Spec. Bull. L. 3 pp.

1891

The mignonette disease. Garden and Forest 4: 33.
Nematodes attacking Bouvardias. Garden and Forest 4: 57.
More nematodes. Garden and Forest 4: 153.
The hydrangea blight. Garden and Forest 4: 177.
Mildew on sweet alyssum and radish. Garden and Forest 4: 189.
Decay spots upon leaves. Garden and Forest 4: 201, 202.
Southern Mississippi floral notes. Garden and Forest 4: 250, 251.
An abundant rust. Garden and Forest 4: 262.
An orchid anthracnose. Garden and Forest 4: 309.
Are fungicides abused? Garden and Forest 4: 359.
Pelargonium blight. Garden and Forest 4: 453.
Nematodes in Zinnias. Garden and Forest 4: 453.
Hollyhock diseases. Garden and Forest 4: 477.
The cranberry scald. Garden and Forest 4: 525, 526.
Damping off. Garden and Forest 4: 549.
A chrysanthemum blight. Garden and Forest 4: 560.
Bacterial disease of celery. Garden and Forest 4: 584.
Rust of carnations. Garden and Forest 4: 596.
Gall-worms injuring the roses. Garden and Forest 4: 608.
A new anthracnose of peppers. Bull. Torrey Club 18: 14, 15.
(With D. G. Fairchild) Influence of moisture upon dehiscent fruits. Bull. Torrey Club 18: 81–85.
A strange thing in peppers. Bull. Torrey Club 18: 151.
The giant sundew heliotropic. Bull. Torrey Club 18: 212, 213.
Intra-carpillary pistils and other floral derangements. Bull. Torrey Club 18: 246–249.
Notes upon *Epigaea repens*. Bull. Torrey Club 18: 249, 250.
A new egg-plant disease. Bull. Torrey Club 18: 302, 303.
A double-headed Rudbeckia. Bull. Torrey Club 18: 304.
What the station botanists are doing. Bot. Gaz. 16: 288–291.
Bacteria of the melons. Bot. Gaz. 16: 303–305.
Notes upon Peronosporeae for 1891. Bot. Gaz. 16: 338–340.
Papers on fungi injurious to fruits and fungi injurious to garden crops, read before the Ohio State Horticultural Society, December, 1890.

Botany at the Washington meetings. Amer. Nat. **25**: 914–916.
The migration of weeds. Proc. Amer. Assn. Adv. Sci. (1890): 304–312.
The anthracnoses and their relations to horticulture. Proc. N. J. State Hort. Soc., 16th Ann. Meeting (1890): 56–66.
Field experiments with soil and black rots of sweet potatoes. N. J. Agr. Coll. Exp. Sta. Spec. Bull. M. 19 pp.
Destroy the black knot of plum and cherry trees. An appeal. N. J. Agr. Coll. Exp. Sta. Bull. 78. 14 pp.
Report of the botanical department. Rept. N. J. Agr. Exp. Stations (1890): 323–333.

1892

Notes upon *Monilia fructigena*, Pers. and spore germination. Bull. Torrey Club **19**: 5–7.
Sweet potato blossoms. Bull. Torrey Club **19**: 22.
Eastern and western weeds. Bull. Torrey Club **19**: 43–46.
Parasitic fungi as related to variegated plants. Bull. Torrey Club **19**: 84–88.
Weeds at the World's Columbian Exposition. Bull. Torrey Club **19**: 131.
A century of American weeds. Their root systems tabulated. Bull. Torrey Club **19**: 141–147.
Anthracnose in bean-seeds. Garden and Forest **5**: 18.
Alternanthera leaf-blight. Garden and Forest **5**: 56, 57.
Fungous troubles in the cutting beds. Garden and Forest **5**: 91, 92.
Petunia blight. Garden and Forest **5**: 141.
"Falling" of egg-plant seedlings. Garden and Forest **5**: 164.
Foliar nematodes. Garden and Forest **5**: 234.
Plum-flower blight. Garden and Forest **5**: 248.
Blights of variegated Pelargoniums. Garden and Forest **5**: 353.
Southern tomato blight at the North. Garden and Forest **5**: 379–381.
Fungous and other rose troubles. Garden and Forest **5**: 406, 407.
Tomato diseases. Garden and Forest **5**: 465.
Decay of quince fruit. Garden and Forest **5**: 477.
Anthracnose of the pear. Garden and Forest **5**: 501.
Diseases of the carnation. Garden and Forest **5**: 594, 595.
Bacterial disease of beans. Garden and Forest **5**: 620.
Some fungi common to wild and cultivated plants. Bot. Gaz. **17**: 113–118.
Cedar trees and apple rust. Amer. Monthly Micr. Journ. **13**: 122.
The influence upon crops of neighboring wild plants. Proc. N. J. State Hort. Soc., 17th Ann. Meeting (1891): 110–122.
Notes upon bacteria of cucurbits (Abstr.). Proc. Amer. Assn. Adv. Sci. (1891): 315, 316.
A new Nectria (Abstr.). Proc. Amer. Assn. Adv. Sci. (1891): 316.
Notes upon an anthracnose (Abstr.). Proc. Amer. Assn. Adv. Sci. (1891): 316, 317.
A section of botany in the American Association. Bot. Gaz. **17**: 25, 26. Also in Science **19**: 81.
Check list of American weeds, in the order of Patterson's list, exclusive of sub-tropical Florida. New Brunswick, N. J.
Fungi injurious to weed seedlings. Proc. Soc. Prom. Agr. Sci., 13th Ann. Meeting (1892): 145–148.
Report of the botanical department. Rept. N. J. Agr. Exp. Stations (1891): 235–349.
(With J. B. Smith) Spraying for insect and fungous pests of the orchard and vineyard. N. J. Agr. Coll. Exp. Sta. Bull. 86. 20 pp.
Some fungous diseases of the quince fruit. N. J. Agr. Coll. Exp. Sta. Bull. 91. 16 pp.
Some fungous diseases of the celery. N. J. Agr. Coll. Exp. Sta. Spec. Bull. Q. 12 pp.
The southern tomato blight. Miss. Agr. Exp. Sta. Bull. 19. 12 pp.

1893

Quince diseases (Abstr.). Bot. Gaz. 18: 25, 26.
New Jersey Peronosporeae (Abstr.). Bot. Gaz. 18: 26.
Weed seeds (Abstr.). Bot. Gaz. 18: 26.
A new form of Exobasidium (Abstr.). Bot. Gaz. 18: 348.
A century of American weed seeds. Bull. Torrey Club 20: 51–55.
A study of solanaceous anthracnoses. Bull. Torrey Club 20: 109–112.
Identity of anthracnose of the bean and watermelon. Bull. Torrey Club 20: 246–250.
Some new weed fungi. Bull. Torrey Club 20: 250–252.
Dropsical Pelargoniums. Bull. Torrey Club 20: 391–393.
Notes upon a new Exobasidium. Bull. Torrey Club 20: 437–440.
The Solandi process of sun printing. Bull. Torrey Club 20: 485–488.
Heliotropism of the common mallow. Bull. Torrey Club 20: 489, 490.
Fatal club-root of turnips. Garden and Forest 6: 78, 79.
A serious filbert disease. Garden and Forest 6: 134.
An observation on fruit decays. Garden and Forest 6: 342.
The rust of mountain ash. Garden and Forest 6: 508.
Fungi parasitic indicate kinship. Science 22: 203.
Blight of ornamental ferns. Amer. Florist 9: 766.
Plasmopora of *Trapaeolum majus* (Abstr.). Proc. Amer. Assn. Adv. Sci. (1892): 221.
Secondary spores of anthracnoses (Abstr.). Proc. Amer. Assn. Adv. Sci. (1892): 221.
A bacterium of Phaseolus (Abstr.). Proc. Amer. Assn. Adv. Sci. (1892): 221, 222.
Fruit decay. Proc. N. J. State Hort. Soc., 18th Ann. Meeting (1892): 131–136.
Potatoes by the direct method. Proc. Soc. Prom. Agr. Sci., 14th Ann. Meeting (1893): 64–68.
Report of the botanical department. Rept. N. J. Agr. Exp. Stations (1892): 275–386.
Club-root of cabbage and its allies. N. J. Agr. Coll. Exp. Sta. Bull. 98. 16 pp.

1894

(With D. G. Fairchild) Sweet-potato black rot (*Ceratocystis fimbriata*, Ell. & Hals.). Journ. Mycol. 7: 1–11.
Blight of garden pinks. Amer. Florist 10: 5, 6.
Begonia diseases. Amer. Florist 10: 117.
Chrysanthemum leaf spot. Amer. Florist 10: 263.
The mint rust upon the variegated balm. Bull. Torrey Club 21: 40, 41.
Club-root in common weeds. Bull. Torrey Club 21: 76–78.
Shrinkage of leaves in drying. Bull. Torrey Club 21: 129–131.
Pistillodia of Podophyllum stamen. Bull. Torrey Club 21: 269.
Peculiar "range" in an autoecious Uromyces. Bull. Torrey Club 21: 311–313.
Other poisonous plants. Bot. Gaz. 19: 200.
Weather versus injurious fungi. Proc. Soc. Prom. Agr. Sci., 15th Ann. Meeting (1894). Agr. Sci. 8: 292–297.
Sunshine through the woods. Pop. Sci. Monthly 45: 313–322.
A serious blight of Cosmos. Garden and Forest 7: 464, 465.
The shrinkage of leaves in drying (Abstr.). Proc. Amer. Assn. Adv. Sci. (1893): 257, 258.
The Solandi printing applied to botanical work (Abstr.). Proc. Amer. Assn. Adv. Sci. (1893): 258.
Bacteria in some of their relations to crop growing. Proc. N. J. State Hort. Soc., 19th Ann. Meeting (1894): 186–196.
Report of the botanist. Rept. N. J. Agr. Exp. Stations (1893): 289–436.

1895

The cherry fruit mold. Garden and Forest 8: 137, 138.
Strawberry leaf curl. Garden and Forest 8: 148.

Aerial roots of carnations. Garden and Forest **8**: 158, 159.
Notes upon poisonous plants. Garden and Forest **8**: 172.
Irrigation in New Jersey. Garden and Forest **8**: 518.
Notes on agriculture (I.). Science, n. ser. **1**: 376–379.
Notes upon agriculture (II.). Science, n. ser. **1**: 509, 510.
Notes on agriculture (III.). Science, n. ser. **1**: 680–682.
Notes on agriculture (IV.). Science, n. ser. **2**: 12.
Notes on agriculture (V.). Science, n. ser. **2**: 68.
How to distinguish fungous diseases of carnations. Florist's Exchange **7**: 293, 294.
Notes upon *Chalara paradoxa* (Abstr.). Proc. Amer. Assn. Adv. Sci. (1894): 293.
Notes upon a root rot of beets (Abstr.). Proc. Amer. Assn. Adv. Sci. (1894): 293.
Blights and their remedies. Proc. N. J. State Hort. Soc., 20th Ann. Meeting (1895): 100–105.
Report of the botanist. Rept. N. J. Agr. Exp. Stations (1894): 275–419.
Some fungous diseases of beets. N. J. Agr. Coll. Exp. Sta. Bull. 107. 13 pp.
(With J. A. Kelsey) Field experiments with fungicides. (Turnips, cabbage, tomatoes, potatoes and beans.) N. J. Agr. Coll. Exp. Sta. Bull. 108. 32 pp.
Field experiments with potatoes. N. J. Agr. Coll. Exp. Sta. Bull. 112. 20 pp.
(With J. A. Kelsey) Irrigation of garden crops. N. J. Agr. Coll. Exp. Sta. Bull. 115. 16 pp.

1896

Forest fungi. Forester **2**: 25.
The black knot of the wild cherry. Forester **2**: 39, 40.
Notes on agriculture and horticulture (IV.). Science, n. ser. **3**: 398, 399.
Notes upon agriculture and horticulture. Science, n. ser. **3**: 588, 589.
Notes upon agriculture and horticulture. Science, n. ser. **3**: 698, 699.
Notes on agriculture and horticulture. Science, n. ser. **3**: 767.
Notes upon agriculture and horticulture. Science, n. ser. **3**: 834–836.
Reseda lutea moving inland. Bull. Torrey Club **23**: 252.
Dodder on garden vegetables. Garden and Forest **9**: 365, 366.
An outbreak of asparagus rust. Garden and Forest **9**: 394, 395.
Fungous diseases of ornamental plants. Trans. Mass. Hort. Soc. (1895): 22–33.
Plant enemies to the horticulturist. Proc. N. J. State Hort. Soc., 21st Ann. Meeting (1896): 89–92.
Report of the botanist. Rept. N. J. Agr. Exp. Stations (1895): 249–361.

1897

A plant catapult. Bull. Torrey Club **24**: 48–50.
Observations upon a clearing in July. Bull. Torrey Club **24**: 407, 408.
Mycological notes. Bull. Torrey Club **24**: 505–510.
The asparagus rust again. Garden and Forest **10**: 236.
The sycamore blight. Garden and Forest **10**: 257, 258.
Dodder in clover. Garden and Forest **10**: 278.
A renewed outbreak of the asparagus rust. Garden and Forest **10**: 335.
Rusty appearance of elm leaves. Garden and Forest **10**: 417, 418.
Plum-fruit rot. Garden and Forest **10**: 436, 437.
Some fungous diseases of celery. Amer. Gardening **18**: 743.
Root galls of cultivated plants. Florist's Exchange **9**: 754, 755. Also in Amer. Florist **13**: 74, 75; and New Eng. Florist **3**: 291, 292.
Forest fungi. Anthracnose of poplars. Proc. Amer. Forest Assn. **11**: 176–178.
Notes upon bean and pea tubercles. Proc. Soc. Prom. Agr. Sci., 18th Ann. Meeting (1897): 77–81.
New fungi. Proc. N. J. State Hort. Soc., 22nd Ann. Meeting (1897): 40–61.
Report of the botanist. Rept. N. J. Agr. Exp. Stations (1896): 289–429.

Field experiments with potatoes for 1896. N. J. Agr. Exp. Stations Bull. 120. 19 pp.
The fungous foes of the farmer. Pa. Dept. Agr. Bull. 28. 19 pp.

1898

"Spotting" in peaches. Asa Gray Bull. 6: 21–25.
Notes upon the growth of stems after being cut. Plant World 1: 74, 75.
Further notes upon the growth of stems after being cut. Plant World 2: 27–29.
Mycological notes. Bull. Torrey Club 25: 158–162.
Mycological notes.—III. Bull. Torrey Club 25: 329–335.
Two cleistogamous parasites of the red clover. Bull. Torrey Club 25: 395–397.
Starch distribution as affected by fungi. Bull. Torrey Club 25: 573–579.
Exposure and fungous diseases. Bull. Torrey Club 25: 622–625.
Observations upon the newer botany. Bot. Gaz. 26: 259–264. Also in Plant World 2: 50–58. 1899.
Notes from the plant hospital. Experiments with cabbages. Amer. Gardening 19: 373.
Notes from the plant hospital. Experiments in infecting soil with the potato scab fungus. Amer. Gardening 19: 435, 436.
Notes from the plant hospital. Experiments with tomatoes. Amer. Gardening 19: 468.
Notes from the plant hospital. Experiments with egg-plants. Amer. Gardening 19: 531.
The violet disease. Amer. Florist 13: 310.
Black spot of rose leaves. Amer. Florist 13: 685, 686.
The lily disease. Amer. Florist 13: 882.
Rose leaf blight. Amer. Florist 13: 951.
The black speck of the rose. Amer. Florist 13: 1170.
The carnation fairy ring fungus. Amer. Florist 13: 1256.
The anthracnose of Ficus leaves. Amer. Florist 13: 1287.
Fungous diseases of hollyhocks. Amer. Florist 13: 1342, 1343.
A palm-leaf blight. Amer. Florist 13: 1426.
Starch distribution as affected by fungi (Abstr.). Proc. Amer. Assn. Adv. Sci. (1898): 408, 409.
Half-shade and vegetation (Abstr.). Proc. Amer. Assn. Adv. Sci. (1898): 415.
Influence of wet weather upon parasitic fungi (Abstr.). Proc. Amer. Assn. Adv. Sci. (1898): 416.
President's address. The Society's progress. Proc. Soc. Prom. Agr. Sci., 19th Ann. Meeting (1898): 17–49.
A consideration of forcing in peaches. Proc. N. J. State Hort. Soc., 23rd Ann. Meeting (1898): 117–140.
Report of the botanist. Rept. N. J. Agr. Exp. Stations (1897): 263–394.
The asparagus rust; its treatment and natural enemies. N. J. Agr. Exp. Stations Bull. 129. 20 pp.
The fungous foes of the farmer. Ann. Rept. Pa. Dept. Agr. (1897): 678–692.

1899

Mycological notes IV. Bull. Torrey Club 26: 12–20.
Mycological notes V. Bull. Torrey Club 26: 72–78.
The influence of wet weather upon parasitic fungi. Bull. Torrey Club 26: 381–389.
A new genus of powdery mildews –Erysiphopsis. Bull. Torrey Club 26: 594, 595.
Relative rate of growth of peas and beans. Asa Gray Bull. 7: 38.
Partial sterility of fertile Woodwardia fronds. Plant World 2: 55, 56.
The fairy ring fungus an indirect fertilizer to grass. Plant World 2: 76, 77.
An experiment with sex in hemp plants. Plant World 2: 110.
What are the habitats of *Scutellaria parvula* of Michaux? Plant World 2: 128.
Peculiarities of purslane. Plant World 2: 165, 166.
The new field botany. Pop. Sci. Monthly 56: 98–105.

Root tubercles upon spring and autumn grown legumes (Abstr.). Amer. Nat. 33: 501.
Poisonous toadstools. Amer. Gardening 20: 380, 381.
Root tubercles and nitrogen appropriation. N. J. State Board Agr. (1898): 105-
Field experiments with "nitragin" and other germ fertilizers (Abstr.). Proc. Amer. Assn. Adv. Sci. (1899): 291, 292.
President's address. Experience notes upon plot experiments. Proc. Soc. Prom. Agr. Sci., 20th Ann. Meeting (1899): 19–29.
Results of observations and experiments upon fruits and vegetables. Proc. N. J. State Hort. Soc., 24th Ann. Meeting (1899): 72–87.
Report of the botanist. Rept. N. J. Agr. Exp. Stations (1898): 291–370.
The poisonous plants of New Jersey. N. J. Agr. Exp. Stations Bull. 135. 28 pp.
An outbreak of chrysanthemum rust. N. J. Agr. Exp. Stations Circular.
The fungous foes of fruits. Ann. Rept. Pa. Dept. Agr. (1898): 482–501.

1900

Coloration of leaf for seed distribution. Plant World 3: 22.
Judging by the fruits. Plant World 3: 116–122.
American and English weeds compared. Plant World 3: 171–173.
Notes upon grape mildew (*Plasmopara viticola*, B. & C.). Asa Gray Bull. 8: 78, 79.
Rusts of horticultural plants. Florist's Exchange 12: 60.
Eel worm in roses. Florist's Exchange 12: 84, 85.
Diseases of the rose. Florist's Exchange 12: 333, 334. Also in Amer. Florist 15: 1033–1037.
The rusts of florists' plants. Amer. Florist 15: 1258.
Concentric spore spots (Abstr.). Science, n. ser. 12: 580, 581.
A new species-hybrid, salsify (Abstr.). Science, n. ser. 12: 584.
Experience notes upon plot experiments. Science, n. ser. 11: 726–732.
Genuine starch factories. Pop. Sci. Monthly 56: 716–722.
The rusts of horticultural plants. Trans. Mass. Hort. Soc. (1900): 11–29.
Seven years of experiments with bush beans. Proc. Soc. Prom. Agr. Sci., 21st Ann. Meeting (1900): 119–129.
Concentric spore spots (Abstr.). Proc. Amer. Assn. Adv. Sci. (1900): 276, 277.
Notes upon a new species-hybrid of salsify (Abstr.). Proc. Amer. Assn. Adv. Sci. (1900): 284.
Four ears of sweet corn. Proc. N. J. State Hort. Soc., 25th Ann. Meeting (1900): 108–114.
Report of the botanist. Rept. N. J. Agr. Exp. Stations (1899): 323–419.
Live covers for country homes. N. J. Agr. Exp. Stations Bull. 144. 39 pp.
Fungous foes of vegetable fruits. Pa. Dept. Agr. Bull. 59. 39 pp. Also in Ann. Rept. Pa. Dept. Agr. (1899): 573–605.

1901

The mignonette as class illustration for ascent of sap. Torreya 4: 56.
Diembryony in corn. Torreya 1: 68, 69.
Weeping tomatoes. Torreya 1: 130, 131.
Are the leaves of "simple-leaved Ampelopsis" simple? Torreya 1: 139–141.
Explosive fruits. Torreya 1: 143, 144.
The asparagus rust. Plant World 4: 88–94.
An abnormal mandrake, dandelion and banana. Plant World 4: 134.
The blooming of twining honeysuckles. Plant World 4: 202–205.
Notes upon albinism in sweet corn (Abstr.). Science, n. ser. 13: 247.
Branched broom-rape upon tomato. Rhodora 3: 295.
Plants as water-carriers. Pop. Sci. Monthly 59: 492–496.
Experiments with tomatoes. Proc. Soc. Prom. Agr. Sci., 22nd Ann. Meeting (1901): 58–61.

What our experiment stations have done in originating varieties of plants by crossing, selecting, etc. (Abstr.). Proc. 14th Ann. Convention Assn. Amer. Agr. Colleges and Experiment Stations. U. S. Dept. of Agriculture, Office of Experiment Stations, Bull. 99: 143, 144.

Some results obtained in cross-breeding of plants. Proc. N. J. State Hort. Soc., 26th Ann. Meeting (1901): 144–148.

Report of the botanist. Rept. N. J. Agr. Exp. Stations (1900): 407–476.

Bean diseases and their remedies. N. J. Agr. Exp. Stations Bull. 151. 28 pp.

1902

The "tendrils" of the Kentucky coffee-tree. Torreya 2: 5, 6.

On the behavior of mutilated seedlings. Torreya 2: 17–19.

Fungi injurious to forests. Statement of Work done by Pa. Dept. Forestry (1901–1902): 68–86.

Behavior of mutilated seedlings (Abstr.). Science, n. ser. 15: 407, 408.

Hints from my experiment grounds. Proc. N. J. State Hort. Soc., 27th Ann. Meeting (1902): 117–124.

Report of the botanist. Rept. N. J. Agr. Exp. Stations (1901): 385–459.

1903

Barn plans and outbuildings. Revised by E. C. Powell. xvi + 385 pp. New York.

(With J. A. Kelsey) Report of the botanist. Rept. N. J. Agr. Exp. Stations (1902): 377–422.

(With J. A. Kelsey) Some of the newer fungicides. N. J. Agr. Exp. Stations Bull. 167. 15 pp.

1904

Blighting of blossoms. Amer. Florist 19: 1093.

(With J. A. Kelsey) Report of the botanist. Rept. N. J. Agr. Exp. Stations (1903): 461–554.

(With J. A. Kelsey) Experiments in crossing sweet corn. A new variety: The Voorhees Red. N. J. Agr. Exp. Stations Bull. 170. 22 pp.

Free distribution of experiment station seeds. N. J. Agr. Exp. Stations Bull. 179. 18 pp.

1905

(With E. J. Owen and J. K. Shaw) Report of the botanist. Rept. N. J. Agr. Exp. Stations (1904): 449–553.

Seed distribution of 1904 and for 1905. N. J. Agr. Exp. Stations Bull. 191. 19 pp.

1906

(With E. J. Owen and J. K. Shaw) Report of the botanist. Rept. N. J. Agr. Exp. Stations (1905): 425–525.

Breeding sweet corn—Co-operative tests. N. J. Agr. Exp. Stations Bull. 192. 30 pp.

1907

(With E. J. Owen) Report of the botanist. Rept. N. J. Agr. Exp. Stations (1906): 371–514.

Station novelties in truck crops. Further distribution of seeds. N. J. Agr. Exp. Stations Bull. 199. 30 pp.

Forest trees of New Jersey. N. J. Agr. Exp. Stations Bull. 202. 52 pp.

Novelties in vegetable fruits. General trial for 1908. N. J. Agr. Exp. Stations Bull. 209. 24 pp.

1908

(With E. J. Owen and N. D. Shore) Report of the botanist. Rept. N. J. Agr. Exp. Stations (1907): 259–386.

Vegetable-fruit seed distribution for 1909. N. J. Exp. Stations Bull. 218. 28 pp.

1909

(With E. J. Owen and N. D. Shore) Report of the botanist. Rept. N. J. Agr. Exp. Stations (1908): 181–301.

Fungi of native and shade trees. Rept. N. J. Forest Park Reservation Comm. 4: 1–120.

1910

(With E. J. Owen, B. H. A. Groth, and N. D. Shore) Report of the botanical department. Rept. N. J. Agr. Exp. Stations (1909): 269–350.

1911

Geometrical figures in plant breeding. Amer. Breed. Mag. 2: 217–220.

(With E. J. Owen, B. H. A. Groth, and Mary Robinson) Report of the botanical department. Rept. N. J. Agr. Exp. Stations (1910): 221–295.

1912

Shade-induced uprightness in the seaside spurge. Torreya 12: 262.

(With B. H. A. Groth, E. J. Owen, Mary Robinson, and Mathilde Groth) Report of the botanical department. Rept. N. J. Agr. Exp. Stations (1911): 313–399.

The elongation of the hypocotyl. N. J. Agr. Exp. Stations Bull. 245. 32 pp.

1913

(With B. H. A. Groth, E. J. Owen, Mary Robinson, Mathilde Groth, and Marion T. Pleasants) Report of the botanical department. Rept. N. J. Agr. Exp. Stations (1912): 349–417.

1914

(With E. J. Owen, B. H. A. Groth, Mathilde Groth, and Marion T. Pleasants) Report of the botanical department. Rept. N. J. Agr. Exp. Stations (1913): 537–629.

1915

(With B. H. A. Groth, E. J. Owen, Marion T. Pleasants, and Mathilde Groth) Report of the botanical department. Rept. N. J. Agr. Exp. Stations (1914): 295–338.

1916

Tickle-grass tumblers. Torreya 16: 226–228.

(With J. W. Shive and E. J. Owen) Report of the department of botany. Rept. N. J. Agr. Exp. Stations (1915): 261–296.

1917

"Peanuts!" Torreya 17: 77–80.

Weight of seeds as related to their number and position in the pod. Torreya 17: 101, 102.

(With E. J. Owen) Influence of position of grains on the cob on the growth of maize seedlings. Journ. Amer. Soc. Agron. 9: 267–274

Degenerate plants. Journ. Hered. 8: 270–276.

(With E. J. Owen) Environment of seeds and crop production. Plant World 20: 294–297.

(With S. A. Waksman) The influence of soil temperature upon seedling corn. Soil Science 3: 393–398.

(With J. W. Shive, E. J. Owen, and O. C. Schultz) Report of the department of botany. Rept. N. J. Agr. Exp. Stations (1916): 433–463.

1918

Color in vegetable fruits. Journ. Hered. 9: 18–23.

Reciprocal breeding in tomatoes. Journ. Hered. 9: 169–173.

Abortiveness as related to position in the legume. Proc. Soc. Prom. Agr. Sci., 38th Ann. Meeting (1917): 68–72.

W... E. J. Owen, O. C. Schultz, J. W. Shive, J. R. Neller, M. I. Wolkoff, W. H. Martin, ...d R. L. Bancroft) Report of the department of botany. Rept. N. J. Agr. Exp. ...ations (1917): 371–424.

1919

Po... ...le correlations concerning position of seeds in the pod. Bot. Gaz. 67: 243–250.
Re... ...t of department of botany. Rept. N. J. Agr. Exp. Stations (1918): 197–201.

Date unknown

Rus..., smuts, ergots and rots. Some of the diseases that seriously affect field crops, ...egetables and fruit. Remedies that have proved successful.

ABSORPTION OF MOISTURE BY GELATIN IN A SATURATED ATMOSPHERE[1]

CHARLES A. SHULL AND S. P. SHULL

A great deal of work has been done to determine the relation of colloidal matter to water, gelatin being a favorite substance for such studies. However, one finds but few attempts to determine the water relations established when the colloidal material is exposed to an atmosphere saturated with water vapor. The earliest observations of a difference in behavior of colloids toward water and water vapor are credited to Volbehr (5). The main work dealing with this subject is a paper by von Schröder (3), who claims that gelatin absorbs much more water when placed in liquid water than when exposed to a vapor-saturated atmosphere. The data presented in his paper were afterwards used as a basis for a theoretical discussion by Bancroft (1), who attempted an explanation of the observed phenomena, but without any apparent attempt to verify von Schröder's results. One finds in the recent literature occasional reference to these papers, as in Czapek (2). Here Czapek (p. 42) adopts Bancroft's explanation of the supposed difference between the vapor pressure of the colloid and that of the mass of water which saturates the atmosphere about the colloid.

For the sake of clearness it will be advantageous to state briefly the results of von Schröder's investigations as given in section VII of his paper, which is entitled "Ein Beitrag zur Thermodynamik der Quellung" (*l.c.*, pp. 109–117).

In the first place, gelatin absorbs water very rapidly from liquid water. A piece of gelatin weighing 0.801 g., and which contained 17.6 percent of hygroscopic water, took up moisture as shown in table 1.

TABLE 1. *Absorption of Water by Gelatin from Liquid Water*

Time	Intake in Grams	Gain Percent*
5 mins.	2.282	336.1
10 mins.	2.934	432.1
20 mins.	3.669	540.3
30 mins.	4.072	599.7
40 mins.	4.300	633.3
50 mins.	4.415	650.2
60 mins.	4.506	663.6
2 hrs.	4.941	727.7
24 hrs.	6.911	1018.
48 hrs.	7.734	1039.

* Calculated on absolute dry weight of gelatin disc, 0.679 g.

[1] Contributions from the Botanical Laboratories of the University of Kentucky, No. 3.

But if a similar piece of gelatin is placed in a saturated atmosphere, moisture equilibrium between gelatin and water is reached at a much lower percentage of intake, as shown in table 2. In this case the air-dry gelatin disc weighed 0.904 g.

TABLE 2. *Absorption of Water by Gelatin in a Saturated Atmosphere*

Time	Intake in Grams	Gain Percent
1 day	0.154 g.	17.08
2 days	0.218	24.10
3 days	0.277	30.69
4 days	0.294	32.56
5 days	0.347	38.21
7 days	0.357	39.52
8 days	0.366	40.52
15 days	0.372	41.18
17 days	0.368	40.74
18 days	0.369	40.80
20 days	0.374	41.41

These figures make it appear that equilibrium was reached at about the end of a week, at a little over 40 percent of absorption.

When the gelatin was first soaked in water till nearly saturated, and then brought into a saturated atmosphere, there was continuous loss of water from the gelatin. Thus a piece of gelatin weighing 0.433 g. was soaked until it weighed 5.092 g. It was then placed in a chamber with a supposedly saturated atmosphere. The behavior is shown in table 3. The first three columns to the left, except the top line, are taken from von Schröder, and the two columns to the right are from Bancroft's discussion of the same experiment, with a correction made by omitting the dashes in Bancroft's table, and lifting the figures into correct alignment with the time intervals.

TABLE 3. *Loss of Water by Gelatin in a Saturated Atmosphere*

Time	Loss in Weight in G.	Loss Percent	Weight of Water in Gelatin in G.	Percentage Absorbed Water Remaining
0 day	——	——	4.659	1,076
1 day	0.259	6.29	4.400	1,016
2 days	0.337	7.82	4.332	998
3 days	0.383	8.87	4.276	988
4 days	0.418	9.68	4.241	979
5 days	0.929	21.50	3.730	861
7 days	1.313	30.45	3.346	759
9 days	1.972	45.63	2.687	621
11 days	2.571	59.48	2.088	482
14 days	3.175	73.46	1.484	343

The percentages in column three are not calculated with great accuracy, but are presented exactly as in the original. The data indicate that there is continuous loss of water from the gelatin, although the air on all sides is assumed to be saturated. The behavior implies a contradiction to the second law of thermodynamics. Such an evaporation of water from one

part of the system to another under the conditions could take place only if the colloidal matter had a higher vapor pressure than the liquid water; and as the water evaporated from the colloidal mass, it would have to condense at the surface of the liquid water. Bancroft's explanation of the higher vapor pressure is based upon the shape and size of the water droplets in the gelatin. They are assumed to be round, and it is held that water evaporates more readily from a curved surface than from a flat one. The droplets of water are so minute that the curvature of the surface of each droplet is quite sharp; this results in a vapor pressure higher in the colloid, and a consequent distillation of water from it to the liquid phase of the system. The distillation should go on until in some way or other the vapor pressure throughout the system reaches equilibrium.

Being engaged in the study of the relation of certain colloidal organic substances to water, we have had occasion to perform some experiments which led to a repetition of some of von Schröder's work. However, it was not possible to tell from von Schröder's discussion just how he set up his experiments, how he controlled the temperature, and how he secured and maintained saturation. In a number of ways the discussion leaves one in the dark, and we were compelled therefore to work out a method of investigation which no doubt differs in a number of ways from von Schröder's. The methods employed are briefly stated.

Materials and Methods

The gelatin used in the experiments to be recorded here was the Gold Label gelatin commonly handled by dealers. No attempts were made to purify it in any way; for, although pure substances are to be preferred in original work of any kind, we felt justified in using the gelatin in its commercial condition because the experiments we were trying to repeat had been carried on with unpurified gelatin. There is no doubt that von Schröder's gelatin as well as ours contained acids, and that in both cases salts were present. We could have neutralized our gelatin with some inorganic base, with subsequent dialysis until it was salt-free. This would have given us a purer gelatin, but we could not then have made a direct comparison between our own and von Schröder's results. It seemed to us best therefore to repeat the experiments with ordinary gelatin, as the differences between the two substances would likely be less than if we used any purification method to remove acids and salts.

During the earlier tests the gelatin was prepared by dissolving it at gentle heat in distilled water, after which it was poured into petri dishes which had been slightly smeared with glycerol to prevent the gelatin from sticking to the glass; but as the glycerol is hygroscopic, this method was abandoned to avoid contamination of the gelatin with glycerol. Mercury was used as an agent to prevent the gelatin from sticking to the glass during drying. In this way sheets of gelatin of desired thickness could be secured,

and these sheets were cut into disks before they became entirely dry, while still slightly pliable, and the disks were dried out in contact with air until weight loss ceased. During this preparation the gelatin was carefully protected from dust to reduce chances of mold or bacterial infection.

The disks were exposed to a saturated atmosphere in small wide-mouthed bottles. The bottles were arranged with a layer of mercury in the bottom sufficient to sink them. Over the mercury was a layer of water. The gelatin disks were suspended over the water, just as near the water surface as practicable, in shallow paper baskets which were attached by threads and wax to the center of the rubber cork which closed the bottle. The rubber cork was shellacked upon its inner and outer surfaces to protect it from water, probably an unnecessary precaution.

To control the temperature the bottles were sunk in a Freas thermostat which was set to run at 26° C., and which showed no deviation with an ordinary chemical thermometer during the five months while the tests were run. It was found necessary to control the growth of bacteria and molds on the gelatin, and this was accomplished by the use of small pieces of thymol in the water. The bottles were usually placed in the thermostat for some time before the gelatin was introduced. This allowed the air to become more nearly saturated. Then the weighed disks were put into the baskets. At intervals which were purposely made infrequent so as not to interfere with the saturation of the air, the disks were removed carefully and quickly to weighing bottles and weighed. The greatest care was taken to keep the disks from drying out during weighing, and to keep the air to which they were exposed during intake intervals from becoming unsaturated. The bottles were always corked and returned to the thermostat during weighings. It was noted that there was always condensation of vapor on the walls of the weighing bottles, so that it was not possible to prevent all losses of water.

RESULTS

In all cases it was found that much more water was absorbed by the gelatin from the atmosphere than von Schröder had observed. During the preliminary tests in one instance there was a regular intake of water which continued for weeks, and which had reached an intake of 250 percent of the weight of gelatin when it was accidentally overturned by the laboratory attendant, and the experiment was thus brought to an abrupt end. A considerable number of disks were started, some with and some without thymol. The rate of intake was apparently about the same during the first several days, but the disks exposed without thymol would always suffer in time with bacterial or mold infections. Usually after about three days the uncontrolled disks had to be discarded. The indications were that the thymol itself was not noticeably accelerating the rate of water intake. Plotted curves practically coincided during the first several days, with and without control.

One typical example of the intake has been chosen to illustrate the behavior of the gelatin under the given conditions. The gelatin disks weighed 0.787 g. air-dry. The absorption data obtained during 47 days are given in table 4.

TABLE 4. *Absorption of Water by Gelatin in a Saturated Atmosphere.*

Time	Intake in Water	Gain Percent
6.5 hrs.	0.1292 g.	15.27
16.5 hrs.	0.2174	27.62
1.0 day	0.2698	34.28
2.0 days	0.3796	48.23
3.0 days	0.4599	58.43
4.0 days	0.5332	67.75
5.04 days	0.5884	74.76
6.0 days	0.6260	79.54
8.0 days	0.7109	90.20
10.0 days	0.7754	98.52
12.0 days	0.8356	106.17
14.0 days	0.8734	110.97
18.0 days	0.9644	122.54
22.0 days	1.0374	131.81
26.0 days	1.0979	139.50
30.0 days	1.1602	147.42
35.0 days	1.2209	155.13
40.0 days	1.2886	163.73
47.0 days	1.3426	170.59

After the last weighing recorded in table 4 was made, the disks were returned to the bottles and left undisturbed for two months, as they were hard to handle without breaking. On opening them at the close of two months, the disks were found in liquefied condition. No culturing was attempted to determine whether liquefying bacteria might have been present. But the thymol had inhibited development of molds, and it is usually considered that molds are less readily controlled than bacteria. It does not appear to us likely, therefore, that liquefaction was brought about by bacterial action.

The contrast in behavior of gelatin as we have found it, and that reported by von Schröder, is shown graphically in figure 1. The possible cause of this difference will be considered later.

One striking thing which has been noted in regard to water absorption is the regularity of intake. It usually begins rapidly, and becomes continually less rapid as absorption increases, falling off in regular fashion till approaching saturation causes a more rapid decline in the rate of intake. The rate of absorption has been studied particularly with reference to seed colloids soaking in water, and mathematical analysis has given us a formula by which the intake can be closely approximated by calculation.

The same kind of analysis was made of the gelatin absorption from saturated air, and the same formula that was derived from the absorption of water by seeds from liquid water can be used in calculating the curve of absorption of water by gelatin from a saturated atmosphere.

The generalized formula is $y = a \log_{10} (bx + 1) + c$, in which y is the percentage of total intake, and x the time, with a, b, and c constants.

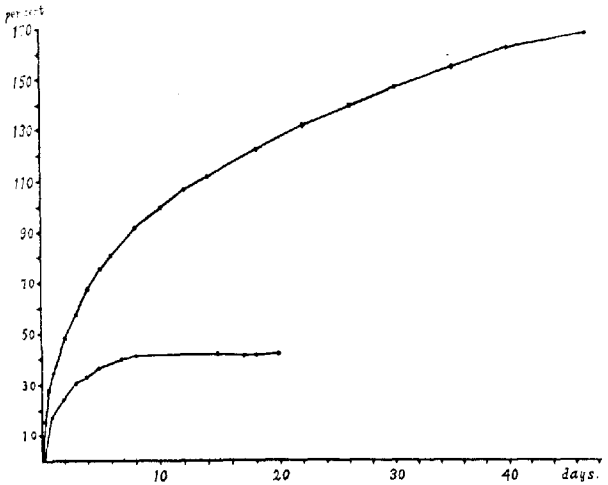


FIG. 1. Curve of moisture intake of gelatin in a saturated atmosphere. Lower curve, from von Schröder's data. Upper curve, from data presented in Table 4.

In the case of seeds we found it necessary to use two or even three curves to approximate the experimental data (4). Similarly it is necessary to use two equations for curves joining in a common tangent value to express the gelatin absorption curve.

The first part of the curve, with the values of a, b, and c substituted in the equation, is as follows: $y = 93.4 \log_{10} (0.032x + 1) + 10.413$; while the later part is expressed thus: $y = 141.9 \log_{10} (0.0064x + 1) + 40.82$. These two curves have equal tangents at $x = 209.47$ hrs., at which time the two values for y are, $y_1 = 93.22723$, and $y_2 = 93.22764$, showing a break in the curve of only .00041 per cent. In other words, at the end of about six days, when the gelatin has taken in something less than its own weight of water (93 percent) it requires different values for the constants in the general formula to keep a calculated curve running close to the data. With these two successive curves there is fairly close agreement between the calculated and the observed data as shown in table 5.

The agreement is very good with the exception of the first and the next to the last readings. The data at 960 hours may be in error, although there is nothing in the records to indicate it. It seems scarcely likely that the

data which had been running so regularly during the preceding 500 hours would suddenly rise above the curve, and then drop back again to the curve 168 hours later. If the error involved accidental addition of the water to the gelatin, it should show in the last reading also. If an error was made it was most likely an error in counting the weights, as a reduction of 10 milligrams in the weight would bring the data to 162.46, which would bring fair agreement with the calculated value. But even as the figures stand the agreement is very striking, and shows that water intake goes steadily forward at a rate determined by the conditions of the experiment.

TABLE 5. *Agreement of Calculated and Observed Intake by Gelatin from Saturated Atmosphere*

Time	Data Low	Calculated Intake	Data High
6.5 hrs.	15.27	18.08	
16.5 hrs.		27.61	27.62
24 hrs.		33.53	34.28
48 hrs.		48.16	48.23
72 hrs.	58.43	58.89	
96 hrs.		67.37	67.75
121 hrs.		74.64	74.76
144 hrs.	79.54	80.35	
192 hrs.		90.17	90.20
		Break in curve	
240 hrs.		98.17	98.52
288 hrs.		105.22	106.17
336 hrs.	110.97	111.54	
432 hrs.		122.52	122.51
528 hrs.	131.81	131.82	
624 hrs.	139.50	139.93	
720 hrs.		147.08	147.42
840 hrs.		154.98	155.13
960 hrs.		161.99	163.73
1,128 hrs.	170.59	170.62	

The actual rate of intake has been measured at several points by measuring the tangents to the calculated curve, and we give the rate of intake in grams per minute.

When $y = 25$ percent, velocity of intake is .015101.
When $y = 30$ percent, velocity of intake is .013348.
When $y = 35$ percent, velocity of intake is .011672.
At the break, $y = 93$ percent, velocity of intake is .002808.

The rate at the time the break occurred was approximately one fifth of the rate when 25 percent had been absorbed. The steady fall in the rate of intake should be noted. These rates are very much lower, of course, than when gelatin is immersed in water, and must depend partly at least on the surface-volume relation of the particular pieces of gelatin used. One would expect a thin, flat piece of gelatin to absorb more rapidly than an equal mass in spherical form.

An important difference between the curve of absorption as shown for gelatin in saturated vapor and that obtained for seeds in water should be noted. The absorption curve for Xanthium seeds shows a break at about 35 percent due to approaching saturation. The gelatin curve here presented shows no such break due to approaching saturation, but maintains a slowly decreasing rate over long periods of time, with remarkable regularity.

Discussion

The data which are presented indicate that gelatin absorbs much more water from a saturated atmosphere than was found by von Schröder. And an examination of his data leads one to suspect that he did not maintain a saturated atmosphere. It is not so easy to see in table 2, but in table 3, which records the loss of water from saturated gelatin, it is rather easily detected. If the behavior in this case were normal, we should find the loss largest during the first 24 hours, because the difference in moisture equilibrium was greatest at the beginning of the experiment. Each day thereafter should show less and less daily loss because of the closer and closer approach of equilibrium conditions. This, however, is not the case in his data. On the first day the loss is 0.259 g., on the second day 0.078 g., on the third day 0.046 g., on the fourth day 0.035 g., and on the fifth day 0.511 g. Counting average daily loss, there was nearly twice as large average daily loss at the end of five days as at the end of the first four days. And at the end of 14 days the average daily loss was still more than double that at the end of the first four days. From the fifth day on, the loss is always much more rapid than during the second, third, and fourth days. This would make it appear very probable that the gelatin was losing water into an unsaturated atmosphere.

And if the atmosphere is unsaturated in this case, it probably was unsaturated in the experiments, the data of which are recorded in table 2. It is a very difficult matter to produce and maintain conditions of saturation, and there is not much doubt that the frequent opening of the chamber for weighing allowed the atmosphere to fall considerably below the saturation point. There is nothing in von Schröder's discussion to show how he handled his materials. Even in our own work we can not be certain that complete saturation was procured and maintained at all times. But the results would indicate that we came nearer to it than did von Schröder.

We feel that the amount of work done is insufficient to show that colloids do not exhibit the phenomenon to which von Schröder's work called attention. Even though we have shown that gelatin takes up from saturated vapor much more water than was formerly supposed, it may still be true that colloids show a difference in behavior toward water in liquid and in gaseous form. Much of the difference in the actual amount of water taken in must be related to the filling of minute lacunae when immersed in water, and the saturation of the gelatin around the lacunae only, when exposed to

vapor. The vapor pressure of a saturated colloid may actually be greater than that of a flat surface of water, and the colloid be able therefore to distil water into the saturated atmosphere which is common to both. Whatever the truth may be in regard to this point, it seems to us unfortunate that a theory of physical chemistry should be based upon a single piece of work which shows somewhat gross irregularities in the data, without any attempt to confirm the original findings.

The experience we have had with gelatin in saturated atmosphere, with conditions controlled as carefully as possible, at least suggests the desirability of a reinvestigation of the relation of the vapor pressure of colloids to that of the vapor pressure of water, before we try to establish or accept theories which attempt to explain this relation. It might be found that there is little to explain.

THE UNIVERSITY OF KENTUCKY,
LEXINGTON, KY.

LITERATURE CITED

1. **Bancroft, W. D.** The action of water vapor upon gelatin. Journ. Phys. Chem. 16: 396–406. 1912.
2. **Czapek, F.** Biochemie der Pflanzen. 2d ed. Vol. 1. Jena, 1913.
3. **von Schröder, P.** Über Erstarrungs- und Quellungserscheinungen von Gelatine. Zeitschr. Phys. Chem. 45: 75–117. 1903.
4. **Shull, C. A.** Temperature and rate of moisture intake in seeds. Bot. Gaz. 69: 361–390. 1920.
5. **Volbehr, B. F. K. J.** Untersuchungen über die Quellung der Holzfaser. Kiel, 1896.

SLOW AND RAPID GROWTH[1]

H. S. REED

The growth rate of plants and of plant organs resembles the rate of a monomolecular chemical reaction (Reed, 1920 *a*). Having obtained a mathematical expression of the growth rate, it should be possible to analyze the process into some of its main components. It has been found that the growth rate of certain organisms may be expressed by the differential equation

$$\frac{dx}{dt} = k(a - x),$$

where x represents the size of the organism at time t, a represents the final size attained, and k is a constant of the reaction. The rate at any given time is, therefore, proportional to the amount of growth yet to be made. It is accordingly rapid at the outset and becomes slower as the end of the growth period is reached.

The integral form of this equation is

$$x = a(1 - e^{-kt}),$$

from which the size of the organism at any time may be calculated. If the above assumption is correct, the calculated value of x should not be widely divergent from the observed value for the same time. As a matter of fact, the two values have been found to agree very well. It seems profitable to extend this method of inquiry into different phases of the problem of growth, in the attempt to gain further information on the dynamics of growth.

Measurements of a selected number of shoots on young apricot trees were made throughout the growing season. The mean length of the shoots at each interval of measurement was taken as the observed length at that particular time.

The shoots were of two sorts, and measurements were separately made upon each. The first were on trees which received no pruning; the second were on trees which received, annually, a severe pruning, with the result that the new shoots grew very much more rapidly than those on the unpruned trees. Both classes of trees are in adjoining rows in the orchard and receive the same cultural treatments with the exception of pruning.

At the outset, 50 shoots were selected for each class, but the number was reduced by various accidents during the summer, with the result

[1] Paper 70, University of California, Graduate School of Tropical Agriculture and Citrus Experiment Station, Riverside, California.

that there were 33 shoots in the unpruned class and 28 in the pruned class. In either case the number of variants is large enough to give a satisfactory mean.

TABLE 1. *Mean Length of New Shoots on Pruned and Unpruned Apricot Trees During one Season*

t	On Unpruned Trees		On Pruned Trees	
	x (Observed)	x (Calculated)	x (Observed)	x (Calculated)
weeks	cm.	cm.	cm.	cm.
1	9	10	13	23
2	17	20	37	43
3	25	28	60	61
4	29	36	73	78
5	34	42	88	92
6	42	48	102	105
7	50	54	113	117
8	57	59	121	128
9	63	63	132	137
10	68	67	142	145
11	71	70	148	153
12	77	73	156	160
13	79	76	163	166
14	82	79	174	171
15	83	81	177	176
16	84	83	182	181
17	85	85	186	184
18	86	86	190	188
19	87	88	194	191
20	88	89	197	194
21	89	90	200	196
22	90	91	203	199
24				
25	94	94	208	204
26				
27			210	207

Table 1 contains the observed lengths of the two classes of shoots on the successive weeks of measurement. The mean final length of shoots on the unpruned trees was 94 cm., and that of shoots on the heavily pruned trees was 210 cm. We may let 100 represent the limiting value of x_1 and 218 that of x_2. By a series of approximations the equation

$$x_1 = 100(1 - e^{-.11\,t})$$

was found to be satisfactory for the values of the shoots on the unpruned trees, and

$$x_2 = 218(1 - e^{-.11\,t})$$

for the shoots on the pruned trees. A graphic comparison of these values is given in figure 1.

It will be seen that the only difference between the two integral equations is in the value of the constant a. The value of k, the constant of the reaction, is the same in both cases. The values of x calculated from these

equations (table 1) are seen to be very close to the observed values with few exceptions; the values, therefore, may be assumed to be approximately correct.

A series of values more nearly corresponding to the observed lengths may be obtained by the means employed in another study (Reed, 1920 *b*) of this kind, but the simpler equation gives satisfactorily close values and its use will contribute to clarity of discussion.

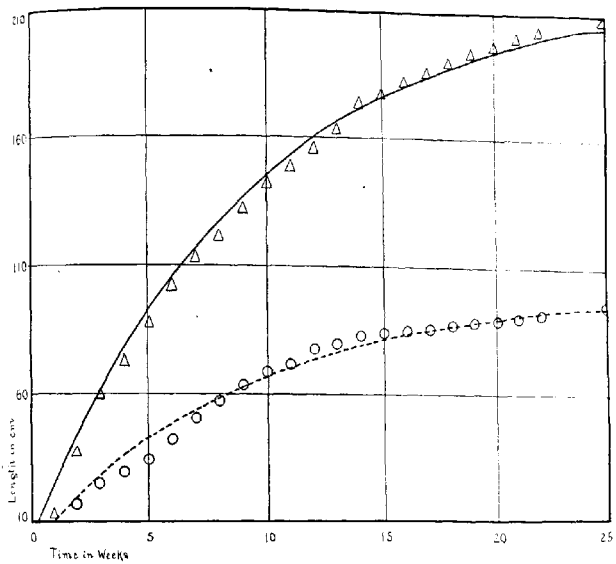


FIG. 1. Curves showing mean length of apricot shoots during one season.
△ △ △, Observed lengths of shoots on pruned trees.
— — —, Length of shoots calculated from $x_2 = 218(1 - e^{-.10t})$.
○○○○, Observed lengths of shoots on unpruned trees.
– – – –, Length of shoots calculated from $x_1 = 100(1 - e^{-.08t})$.

The differential equation, $dx/dt = k(a - x)$, represents rate of growth, *i.e.*, amount of elongation in unit time. If we get the weekly increments in length, we shall have the observed increments in unit time expressed as a rate per week, and can compare them with values calculated from the above differential equation. Since there are inevitable fluctuations in the actual growth rate, it will be better to use "adjusted" values, *S*, of the observed increments. This is a *slope* method of determining the observed values of

dx/dt and has been applied to statistical problems by McEwen and Yule (1919). Its usefulness depends upon the fact that the slope of the chord of a simple curve is approximately equal to that of the tangent at the point midway between the extremities of the chord. The values of S are obtained from $\frac{1}{2}$ (observed length at time $t + 1$ − observed length at time $t - 1$), which represents the average rate between time $t + \frac{1}{2}$ and time $t - \frac{1}{2}$. Figure 2 shows the values so obtained compared with the calculated rate. They show that the rate is at a maximum at the inception of the growth period and follows the course of a curve decreasing exponentially to the end of the period.

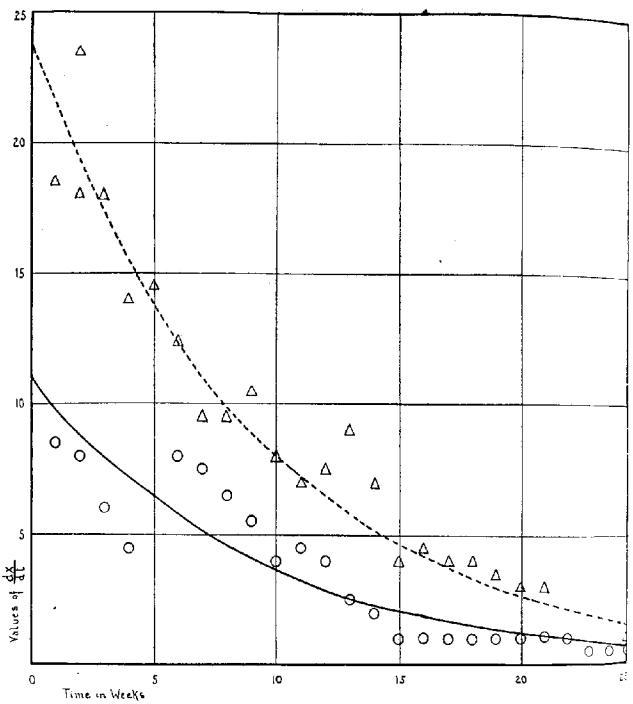


FIG. 2. Curves expressing rate of growth of apricot shoots.

△ △ △, Observed growth increments (S) of shoots on pruned trees.
– – – –, Values of $dx/dt = .11(218 - x_2)$.
○○○○, Observed growth increments (S) of shoots on unpruned trees.
————, Values of $dx/dt = .11(100 - x_1)$.

From these results, it is plain that the quantitative difference between the two classes of shoots existed from the very outset, and that the greater total growth of shoots on the pruned trees was due to their faster growth in the early part of the period. This conclusion accords with the results of Pearl and Surface (1915), who showed that the superior plants in a population are, as a rule, superior from the seedling stage, and that the inferior members of the population are likewise inferior from the beginning.

This raises an important physiological question, *viz.*, How did the pruning of one lot affect the growth process in such a way that they made so much more rapid growth as soon as activity began in the spring? In other words, what happened to cause one lot to grow three times as fast as the other in the second week?

Referring to the differential equation expressing the rate, it will be seen that the rate in unit time is equal to the product of two quantities. The first quantity is k, the constant of the reaction, and the other is $(a - x)$, the difference between a constant and the length of the shoots at time t. The rate of growth of the two classes of shoots differs, then, only by the value of the second factor, *i.e.*, $(a - x)$. From the data, it seems probable that k, the constant of the reaction, is determined by the genetic constitution of the tree. It is well known that its value is determined from

$$k = \frac{1}{t} \log \frac{a}{a - x}.$$

The quantity $a - x$ is, therefore, the one whose value was altered. Now, from the integral equation

$$x = a(1 - e^{-kt})$$

it is easy to see that

$$a - x = ae^{-kt},$$

which means that the values of $a - x$ are equal to the product of a by an exponential function of the time. Since in both the unpruned and the pruned trees the value of e^{-kt} was the same, it is, therefore, plain that the value of $a - x$ is dependent upon the value of a. While the value of a must be, in a measure, determined by hereditary factors, it seems also subject to the influence of outer environmental factors such as those here operative.

In short, the rate of growth of the shoot appears to depend upon its final length. Whatever, therefore contributes to the production of the ultimate length of the shoot influences the rate of growth from the beginning of the season.

The close correspondence between the growth of the shoots and the equations above stated is evidence that their growth is some sort of a catalytic process. According to this view, the organism is the end-product of a process in which a catalyst acts upon a substrate.

LITERATURE CITED

McEwen, G. F., and Michael, E. L. (1919). The functional relation of one variable to each of a number of correlated variables determined by a method of successive approximation to group averages: a contribution to statistical methods. Proc. Amer. Acad. Arts and Sci. **55**: 89–133.

Reed, H. S. (1920 *a*). The nature of the growth rate. Journ. Gen. Physiol. **2**: 515–561.

Reed, H. S. (1920 *b*). The dynamics of a fluctuating growth rate. Proc. Nat. Acad. Sci. **6**: 397–410.

Pearl, R., and Surface, F. M. (1915). Growth and variation in maize. Zeitschr. Indukt. Abstam.- u. Vererbungslehre **14**: 97–203.

CYTOLOGY AND SYSTEMATIC POSITION OF PORPHYRIDIUM CRUENTUM NAEGELI

IVEY F. LEWIS AND CONWAY ZIRKLE

Porphyridium cruentum, named by Nägeli in 1849, has had a systematic history equaled by few plants. It had previously been called at various times Thelepora, Tremella, Sarcoderma, and Byssus. Agardh (cit. Brand) named it *Palmella cruenta*, and under this name Hassall classified it with the Palmellaceae. Indeed, Nägeli himself placed it in this group, and there it was kept by Kützing in his Tabulae Phycologicae (1849–71) under the name given it by Agardh. Rabenhorst seems to have been the first to place it in the Porphyraceae (1868), and he was followed in this four years later by Wood. Cooke in 1884 returned it to the Palmellaceae. Wolle likewise placed Porphyridium in the Chlorophyceae and found it to be identical with *Protococcus miniatus*. On the other hand, Schmitz (cit. Brand) considered it related to the Florideae, and Gaidukov (cit. Engler and Prantl) put it in the Bangiaceae. In 1902 Chodat returned it to the Chlorophyceae and would place it near Schizogonium. West two years later believed that Porphyridium belongs in the Myxophyceae and is allied to Aphanocapsa, while Hansgirg (cit. DeToni) made the genus but a species of Aphanocapsa and called it *A. cruenta*. Oltmanns in 1905 put Porphyridium once more in the Chlorophyceae. He was not certain as to its exact position but placed it supplementary to the Scenedesmaceae. DeToni classified Porphyridium as one of the Myxophyceae belonging to the family Glaucophyceae. Brand in 1908, as a result of his work on this plant, believed that it belongs to the Bangiaceae, and in this he is generally followed by the systematists, Engler and Prantl, West, who changes his original position, and Collins. Tilden, however, keeps Porphyridium in the Myxophyceae. While Kufferath got some results very different from Brand's, he agreed with the latter as to its systematic position, although he suggested that in the contingency of its having no chlorophyll it be placed with the red bacteria. Brand cited Borzi as being in favor of putting Porphyridium with Protococcus, Richter as favoring putting it with Trentepohlia, while Klebs would have it as a questionable member of the Pleurococcaceae.

The descriptions of Porphyridium differ almost as much as its various systematic positions. Nägeli, working unfortunately with dried material, described it as follows:

"Cells flattened, in surface view round or somewhat polygonal from lateral pressure, with a lateral thin confluent sheath, united in one-layered

free-lying families; divisions in varying vertical planes; all generations fully developed and alike; cell contents purple.

"Type *P. cruentum* (*Palmella cruenta* Ag.), the only known species.

"The blood-red gelatinous layer consists of larger or smaller one-layered plates, whose cells seen from the surface appear rounded and mostly somewhat angular. The thickness of the cells is in dry specimens one third to one fifth the breadth. The thin sheaths run together in a structureless jelly in which the cells are imbedded. The sheaths are one third to one fifth, more seldom up to one half, of the lumen. The true wall is very thin.

"The cell content is colored by erythrophyll. It looks beautifully purple and agrees in color with *Porphyra vulgaris*. I could not see a nucleus in it."

On procuring some living material he amended his description somewhat:

"Cells spherical or polyhedric with tolerably thin confluent sheaths, united in a somewhat gelatinous layer; divisions varying in all directions of space or exceptionally only in vertical planes. . . . This genus is distinguished from Palmella by the erythrophyll in the cell content." He added in a note: "Further I saw in the fresh plant, often in every cell, a whitish granule (a chromatophore filling itself with starch), such as the other Palmellaceae possess."

In 1875 Mer found starch in Porphyridium, and in the same year Saint-Léon found no trace of sexual reproduction and only simple multiplication through the division of the vegetative cells. Schnetzler (1878) reported that the red coloring matter disappears when the alga is pickled in a borax solution, leaving the color green, and Nebelung (1878) that the red pigment has a spectrum which may be considered as a modified spectrum of the pigment of Phormidium. Schmitz added considerably to our knowledge of this alga by describing in it a star-shaped chromatophore, which, like those of the Bangiaceae, Bacillariaceae, and Rhodophyceae, contains no starch; and also a colorless centrally located pyrenoid and an eccentric nucleus. Later he reported that "the special cell membrane is repeatedly formed anew on the single cells, the old membrane is torn through on one side and stripped off as a stalk, at first sharply delineated and later becoming more and more formless gelatin." On the other hand, Oltmanns described the cells as being imbedded in formless jelly.

Brand reported that the chromatophore is not typically star-shaped but often in wet weather is round, and that the star-shape, when it does occur, comes from its being indented with the peripherally located granules and vacuoles. These granules he took to be cyanophycin granules, though he records that they are not stainable with acid carmin, which is generally held to be the most typical stain for such granules. The coloring matter, he found, is floridean red and varies only in its intensity. He was unable to find any green modification. The pyrenoid is described as being ring-shaped

and often hard to see, and in "house cultures" it even disappears in most cells. In regard to the nucleus he said: "Although now the existence of a nucleus is *a priori* very probable, I could, after completely dissolving the sheath, never with certainty show one. The nucleus-like structures which one sees in living as well as in fixed stained material, are not only in regard to size, form, and position very variable, but appear sometimes single and sometimes many. All usual methods of staining have given me, through repeated investigations, very uncertain results."

Kufferath, utilizing the technic of bacteriology, was able to get a pure culture of Porphyridium to grow in various gelatinous media. The alga growing thus showed a great increase in size, at times reaching a diameter of 24 μ, and showed somewhat of a variation in its method of division. Two daughter cells sometimes developed within the body of the mother cell, and even tetrads occurred. Kufferath denied the existence of a pyrenoid in Porphyridium and stated that what has been taken for a pyrenoid is an optical effect due to a convergence of the light rays by the plastid. In regard to the nucleus also his findings are quite different from Brand's. He writes: "The nucleus, which has been seen only by Schmitz, is colored by the usual stains; it is oval, somewhat refractive and applied against the cell wall; it is small and we have not been able to distinguish its intimate structure."

A most obvious explanation for this divergence in the results of the various investigators would be furnished if the case of Porphyridium were analogous to that of Protosiphon and Botrydium. Different species of plants, no matter how much alike externally, would hardly give identical results on an intimate investigation, especially if their ancestry were diverse and they had evolved along parallel lines. While it is possible that more than one genus has been investigated under the name of Porphyridium, and this possibility should not be overlooked in future investigation of this much studied but little known alga, the facts at present do not substantiate this hypothesis. The present investigation has often shown in the same plant two characters, each of which has been described and had its existence denied by some of the aforementioned authors, whose views were just the opposite in regard to its accompanying character.

The diameter of Porphyridium in the material studied varies from 5 μ to 9 μ, the smaller cells almost uniformly being in the resting condition. The jelly secreted by each cell forms an individual sheath about that cell and, when division takes place, the two daughter cells are in the same sheath, which follows the constriction of the cells quite intimately, and lengthens as the cells draw apart. The portion of the sheath between the two cells becomes drawn out into a strand or stalk (figs. 10, 11, 39). As these cells were originally within the sheath of the mother cell, which itself was on a stalk, we frequently find the mother stalk branching into two

daughter stalks. However, no case was found of more than two cells being borne on branches on a single stalk, which would indicate that the stalk does not persist through three generations. Indeed, if growth is inhibited, the stalks tend to blend into a common gelatinous sheath and appear as in figure 12. The stalks are elastic. It is quite a common instance for two sister cells to have stalks of different lengths, and in each instance observed the longer stalk was the thinner, as if it had been stretched out. Brand observed that the pressure of the cover glass would flatten out the jelly, which would resume its original shape if the pressure were removed.

Löffler's flagellum stain will show these stalks very well, a little better as a rule if pyrogallic acid be used in place of tannic acid. A good method of proceeding is to place a small amount of rapidly growing alga on a slide and allow it to dry until it has lost all of its water content. It should then be covered with the mordant and heated for ten minutes over a water bath.

Much clearer results, however, have been obtained by allowing the alga to dry as described above and then fixing in the following solution:

Sat. sol. anhydrous ferric bromide in ether ..... 1 part
Molar sol. pyrogallic acid in ether ..... 2 parts

The water in the gelatin will cause the solutes to ionize, and hence ink will be precipitated within the gelatin. This makes a good mordant for gentian violet and safranin. If the jelly has dried too much it can be impregnated with ink by having the fixing agent washed off with water. Another good fixing and staining agent for jelly is:

Sat. sol. gentian violet in 95% alcohol ..... 1 part
Formalin (40% formaldehyde) ..... 1 part

This stains the jelly a dark red or purple and leaves the cell contents colorless.

The chromatophore is typically star-shaped in the resting cell (figs. 12, 13, 18). However, in the cells that are rapidly growing, the enlargement of the cell does not seem to be followed by an equal increase in the size of the chromatophore, so large vacuoles appear at its periphery. Its shape can then be best described as amoeboid.

The chromatophore is of a dark red color, almost that of clotting blood. If, however, the plant is allowed to stand for a short while under water, the red coloring matter can be seen dissolved in the water and the gelatinous mass becomes grass-green.

The centrally located body, which has almost uniformly been called a pyrenoid whenever it was observed, and will be considered such in this paper, is colorless in the living cell and appears only as a light spot in the chromatophore. Unstained it could very readily be mistaken for an artefact due to the refraction of light by the chromatophore. However, the "convergence of light rays" of Kufferath takes Heidenhain's haematoxylin very well and is not indifferent to gentian violet and safranin (figs. 2, 9, 18,

27. The pyrenoid is generally spheroidal in shape, though when the cell starts to divide it lengthens and becomes somewhat angular. As a rule it stains uniformly dark, though at times it appears ring-shaped with a relatively unstained center (figs. 25–27).

A single eccentrically located globule, a trifle smaller than the pyrenoid, has been frequently noted in Porphyridium. It can be seen very easily in the living specimen and has been observed to fragment as the water content of the cell increases, the fragments arranging themselves about the chromatophore. Except in its reaction toward acid carmin it seems to act as if it were cyanophycin. In general, we find, it takes the usual nuclear stains, haematoxylin, gentian violet, and safranin.

Picric acid has, on the whole, given the best results as a fixing fluid. If it is washed out in running water, the chromatophore will be dissolved and the pyrenoid and "nucleus" left without being obscured by any other cell structure. Ten minutes in the acid is enough for the fixation, and from fifteen minutes to twelve hours will do for the washing out of the fixative. Mordanting for one hour in iron alum and staining for a like period in haematoxylin have given the best results with this stain. Staining for ten minutes over a water bath is sufficient for anilin-gentian violet and anilin-safranin, and the specimen can then be decolorized by allowing it to stand over night in methyl alcohol. Another very successful fixative and mordant is:

Pyrogallic acid (25% aqueous sol.)	10 parts
Ferrous sulphate (sat. sol.)	5 parts
Fuchsin (sat. alc. sol.)	1 part

Van Ermengen's osmic acid process has given only fair results. Whenever the material was fixed in either of Flemming's fluids, or when fixed in picric acid and hardened in alcohol, the chromatophore stained so densely that it was impossible to distinguish anything in the cells clearly. Flemming's triple stain has given very fair results.

The chromatin, consisting of a single eccentric granule surrounded by a clear space in the cell (fig. 18), is typical of the resting stage, a stage described by Brand as "wasserarm." The cell, however, if dried, is useless as far as any clear results are concerned. As the cell prepares for division, this granule enlarges and begins to fragment, assuming the various shapes shown in figures 18–27. No hard and fast rule can be laid down for establishing a sequence of forms in this breaking up, as there are many forms which do not fit well into any series that could be arranged out of the others, although some of the shapes occur in many cells. The "U" shape is perhaps the most common (figs. 21, 22), and it is not at all unusual to find the fragments united in a line (figs. 23, 24) or in a ring (fig. 20). Frequently the pieces in drawing apart leave trails which have a striking resemblance to the mitotic spindle (fig. 25), which resemblance seems to be purely accidental. As an end result of this fragmentation the chromatin is distributed in the

form of small elongated granules about the periphery of the chromatophore (figs. 27, 28). These granules then fuse end to end and a well tangled spireme results (fig. 29). A striking thing about this spireme is the way various strands lie parallel to each other. One is greatly tempted to see in this a conjugation or perhaps a splitting of the spireme. However, the members of a pair do not necessarily go to different cells. The spireme breaks into pieces of varying lengths, and these segments frequently withdraw into two distinct masses before the cell has started to constrict. More often, however, the chromatin is constricted in two with the cell (figs. 30, 31), and it is nothing unusual to see strands extending some distance into each daughter cell when the cells are connected only by a narrow isthmus (fig. 32). Two granules of chromatin occur regularly at the poles of the dividing cell at the maximum distance from the plane of constriction (figs. 30, 31, 32). These granules occupy these definite positions too often for this arrangement to be due to a mere fortuitous placing of waste chromatin, though what function is served is not at all clear. In the majority of cases the segments of the spireme in newly divided cells lie alongside the new wall formed by the constriction (fig. 33). If any spindle fibers were present in this division, the technic used caused them to be dissolved, as no traces of them were found. The evidence at present indicates that a typical resting stage is not necessary between successive cell divisions especially if the conditions are just right for rapid growth.

The dividing cells studied came from an agar culture in Chodat-Grintzesco solution. For a culture to thrive it must not be in a liquid medium or kept in the dark. No organic energy-yielding compound was necessary for rapid growth.

In searching for mitosis in a primitive or degenerate plant, the investigator is exposed to the danger which beset the late centrosome hunters, of mistaking a chance resemblance for a homologue. The eccentrically placed globule seems certainly to be chromatin, and whether we call it a nucleus or a nucleolus depends upon the relative flexibility with which we use these terms. In regard to its fragmentation it resembles the nucleolus, though if it is the nucleolus it contains all of the chromatin at this stage, which is not typical. The amount of chromatin apparently increases greatly as the fragmentation progresses, and this increase is too great to be explained by the increase in the precipitation of the stain on the increased surface exposed. Some of the stainable material may come from the fragmented pyrenoid. The chromatin is arranged in a typical spireme, which breaks up into segments of diverse sizes which may safely be considered as analogues of chromosomes. There is no lining up on an equatorial plane or any indication of the segments splitting and having their halves drawn to opposite poles. This method of nuclear division may be recorded as mitotic, but the mitosis is quite primitive and of an exceptional kind.

The bearing of this method of nuclear division upon the systematic posi-

tion of Porphyridium must be uncertain until more is known of the nuclear history of the Bangiaceae. The resting stage is certainly unlike anything known in the Myxophyceae, though the later stages show a certain resemblance to this group. The whole process is a bit too primitive for the Chlorophyceae. In regard to its other characteristics Porphyridium resembles the Bangiaceae, and it would be best to keep it in this group.

The authors wish to thank Dr. W. R. Taylor for the material he supplied.

SUMMARY

1. Divergent results of the various investigators are probably due to their working with plants at different stages of growth rather than to their working on plants of different species.

2. The jelly is homogeneous only after a prolonged period of inactivity of the plant. In growing material the cells are born on gelatinous stalks.

3. The chromatophore is star-shaped only in the resting stages. Its red coloring matter can be extracted, leaving it green.

4. Porphyridium has a distinct, easily stainable, centrally located pyrenoid, which is generally spheroidal though sometimes ring-shaped.

5. In the resting stage Porphyridium has a single eccentric globule of chromatin homologous to a nucleus or nucleolus. Nuclear division is crudely mitotic.

6. Porphyridium had best be kept in the Bangiaceae at present.

BIOLOGICAL LABORATORY,
UNIVERSITY OF VIRGINIA

LITERATURE CITED

1. **Brand, F.** Über das Chromatophor und die systematische Stellung der Blutalge (*Porphyridium cruentum*). Ber. Deutsch. Bot. Ges. **26a**: 413–419. 1908.
2. ——. Weitere Bemerkungen über *Porphyridium cruentum*. Ber. Deutsch. Bot. Ges. **26A**: 540–546. 1908.
3. **Chodat, R.** Algues vertes de la Suisse. Berne, 1902.
4. **Collins, F. S.** Key to the algae. Tufts College Studies, no. 4. 1918.
5. **Cooke, M. C.** British freshwater algae. London, 1884.
6. **DeToni, J. B.** Sylloge Algarum. Vol. 5, Myxophyceae. Padua, 1907.
7. **Engler, A.,** and **Prantl, K.** Die natürlichen Pflanzenfamilien. Nachträge zum I. Teil, 2. Abteilung. Leipzig, 1911.
8. **Hassall, A. H.** British freshwater algae. London, 1845.
9. **Kufferath, H.** Note sur la physiologie et la morphologie de *Porphyridium cruentum* Naegeli (Note préliminaire). Bull. Soc. Roy. Bot. Belg. **52**: 286–290. 1913.
10. **Kützing, F. T.** Tabulae phycologicae. Nordhausen, 1849–1871.
11. — —. Species algarum. Leipzig, 1849.
12. **Mer, É.** La Glycogenèse dans le règne végétal (suite). (Abstr. in Just's Bot. Jahresb. 3: 3. 1875.)
13. **Nägeli, C.** Gattungen einzelliger Algen. Zürich, 1849.
14. **Nebelung, H.** Spektroskopische Untersuchungen der Farbstoffe einiger Süsswasseralgen. (Abstr. in Just's Bot. Jahresb. 6[1]: 199; 343; 628, 629. 1878.)
15. **Oltmanns, F.** Morphologie und Biologie der Algen. Vol. 2. Jena, 1905.
16. **Rabenhorst, L.** Flora Europaea Algarum. Section III. Leipzig, 1868.

17. **de Saint-Léon, V. T.** Sulla fruttificazione della Ceramiee. (Abstr. in Just's Bot. Jahresb. 3: 1007, 1008. 1875.)
18. **Schmitz, F.** Die Chromatophoren der Algen. (Abstr. in Just's Bot. Jahresb. 10: 290–295, 405, 406. 1882.)
19. ——, **and Hauptfleisch, P.** Rhodophyceae. In Engler and Prantl's "Die natürlichen Pflanzenfamilien" I, 2: 298–544. Leipzig, 1897.
20. **Schnetzler, J. B.** Über *Porphyridium cruentum*. (Abstr. in Just's Bot. Jahresb. 6: 396. 1878.)
21. **Tilden, J.** Minnesota algae. Vol. 1. Minneapolis, 1910.
22. **West, G. S.** British freshwater algae. Cambridge, 1904.
23. ——. Cambridge botanical handbooks. Vol. 1, Algae. Cambridge, 1916.
24. **Wolle, F.** Freshwater algae of the United States. Bethlehem, Pa., 1887.
25. **Wood, H. C.** A contribution to the history of the freshwater algae of North America. Philadelphia, 1872.

EXPLANATION OF PLATES

PLATE XX

These photographs were taken with a Gordon's photomicro camera. In figure 1, a Zeiss 2 mm. water-immersion objective and a Bausch and Lomb no. 10 eye-piece were used; in figures 2–12, a Zeiss 1.5 mm. oil-immersion objective and a Zeiss compensating ocular no. 6. The tube length was 160 mm. Magnification, × 400.

FIG. 1. Living cells showing cell division.

FIG. 2. Fixed in picric acid and stained in Heidenhain's haematoxylin.

FIG. 3. Same as figure 2.

FIG. 4. Fixed over a water bath with picric acid and stained with anilin-gentian violet.

FIG. 5. Fixed and mordanted with pyrogallic acid-ferrous sulphate, stained with anilin-gentian violet.

FIG. 6. Fixed as in figure 5. Not stained.

FIG. 7. Fixed as in figure 5. Stained with anilin-safranin.

FIG. 8. Stained by Van Ermengen's osmic acid-silver nitrate process.

FIG. 9. Fixed with tannic acid, stained with anilin-gentian violet.

FIG. 10. Fixed with a solution of pyrogallic acid and ferric bromide in ether, stained with safranin.

FIG. 11. Same as figure 10.

FIG. 12. Fixed in 1 part formalin and 1 part saturated solution of gentian violet in 95% alcohol, counterstained in Heidenhain's haematoxylin.

PLATE XXI

FIGS. 13–17. Living material showing increase in size and cell division. × 1070.

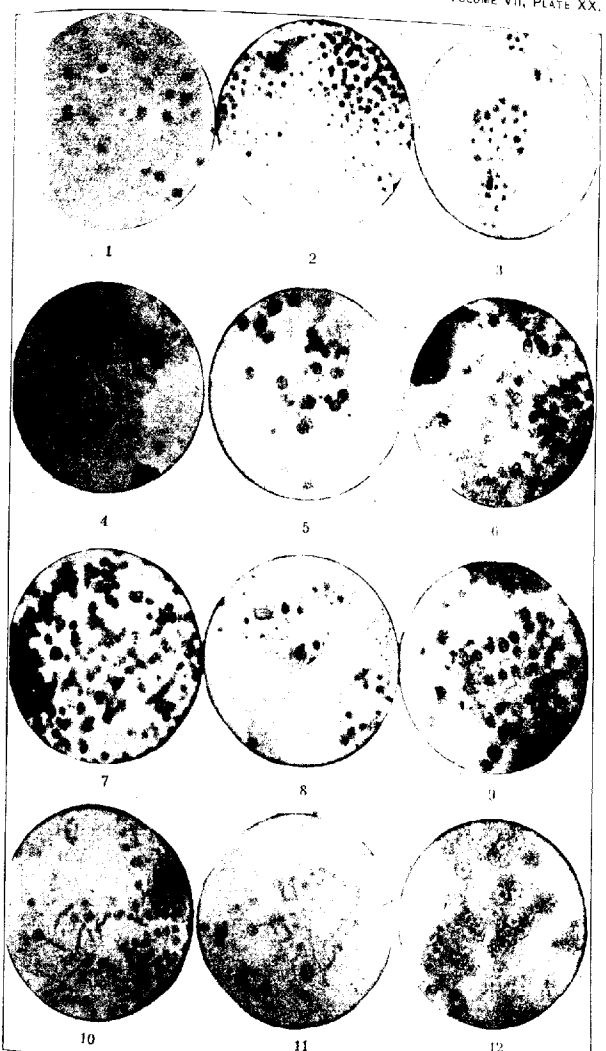
FIG. 18. Resting stage. × 1600.

FIGS. 19–27. Stages showing fragmentation of chromatin and changes in pyrenoid. × 1600.

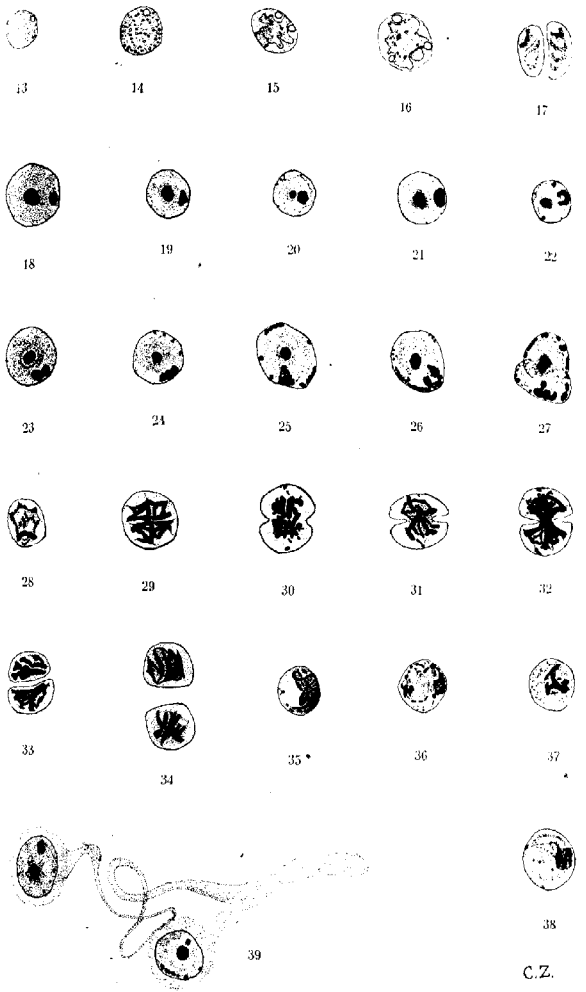
FIGS. 28–34. Stages showing nuclear and cell division. × 1600.

FIGS. 35–38. Stages showing reassembling of chromatin. × 1600.

FIG. 39. Cells connected by stalks. × 1600.



LEWIS AND ZIRKLE: CYTOLOGY AND SYSTEMATIC POSITION OF PORPHYRIDIUM.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SOMATIC CHROMOSOMES IN TRADESCANTIA

LESTER W. SHARP

INTRODUCTION

In 1913 the writer published the results of a study of chromosome behavior in the somatic cells of *Vicia faba*, the principal conclusion reached being that the splitting of the chromosomes is a phenomenon of the prophase. This view was directly opposed to that of Lundegårdh (1910, 1912), Fraser and Snell (1911), and Miss Digby (1910), who had contended that the telophasic alveolation of the chromosomes represents a splitting, and that the chromosomes remain through the ensuing resting stages as double structures. It was pointed out by the writer that this latter interpretation is rendered untenable by two lines of evidence which appear when the various transformations of the chromatin are minutely examined: first, the telophasic alveolation is very irregular and transforms each chromosome into an alveolar and then into a reticular structure which is in no true sense double, although chance arrangement of the vacuoles may often make it appear so; and second, the reticular chromosome, after separating from its fellows in the common reticulum during prophase, gives rise in a peculiar manner to a single (*i.e.*, not double) slender thread in which vacuoles, all or nearly all of them new, appear and develop into the true split.

The theory of telophasic splitting has been restated by Fraser (1914), Digby (1914, 1919), and Nothnagel (1916), who have employed it in the attempt to solve the problem of the heterotypic prophase. This point is one of fundamental importance, and will be taken up in some detail in the discussion.

The present study of the somatic chromosomes of *Tradescantia virginiana* L. was undertaken not only to test the writer's position with respect to the time of chromosome splitting in somatic mitosis, but also, by determining more precisely the nature of the transformation of the chromosomes in the somatic telophase, to ascertain to what extent, if at all, this transformation will aid in the interpretation of the heterotypic prophase. Essentially the same methods were employed as in the former investigation of Vicia. Although the behavior of the chromatin in the two cases is strikingly similar, Tradescantia, so far as could be judged from the preparations obtained, proved to be inferior to Vicia for a study of the late prophases; for the analysis of the critical stages of the telophase and early prophase, however, it turned out to be quite superior, many exceptionally clear figures being obtained. Root tips alone were used.

Among previous works dealing with Tradescantia may be mentioned

those of Strasburger (1900), Miyake (1905), and Farmer and Shove (1905). The first two papers treat of the maturation mitoses. Both Strasburger, in his figures 97–100, and Miyake, in his figures 152 and 153, suggest a process of alveolation in the chromosomes during the heterotypic telophase. Farmer and Shove give an account of both the somatic and the maturation mitoses. They speak of a "vesiculation" of the chromosomes in the somatic telophase, the chromatin becoming a "cloud of fine granules through the linin band"; and describe "broad band-like areas" with the chromatin in a dense "granular aggregation" during the early telophase. These conditions are faintly suggested in their figures 2, 2*a*, 20, and 21. But in none of these investigations have the changes undergone by the chromatin been followed closely enough to afford evidence on the time of chromosome splitting, or on the precise manner of the transformation of the chromosomes into the resting reticulum and of the latter into chromosomes.

Description

In order to give an uninterrupted account of the history of the chromatin through the critical stages—the telophasic transformation of the chromosomes into the resting reticulum and the subsequent condensation of the latter into chromosomes—the description will begin with the metaphase.

Metaphase and anaphase. As is usually the case with long chromosomes, those of Tradescantia are inserted on the spindle by their middle points. Six of them are thus shown in figure 1 (a portion of the chromosome on the right has been cut away). Since no detailed comparison of all the chromosomes of the group has been made, it is not known whether or not this mode of insertion is an invariable one. The free ends of the chromosomes extend out in various directions, but most commonly lie more or less parallel to the axis of the mitotic figure. As Farmer and Shove also observe, the doubleness of the chromosomes reaches its maximum distinctness at this time.

Because of their mode of attachment to the spindle, the chromosomes take the form of V's as they move toward the poles at anaphase (figs. 2, 3). The mottled appearance shown by the chromosomes appears to be due very largely to their uneven contour, though unequal density of the chromatin in various portions of the chromosome may be partly responsible. Nothing which can be called internal granules or chromomeres has been distinguished at this stage, and only occasionally do any vacuoles make their appearance so early. As they reach the poles the chromosomes become much shortened and thickened, and contract into two dense groups in which the limits of the chromosomes can be made out only with considerable difficulty. The new cell plate now begins to be differentiated on the fibers between the two groups.

Telophase. After remaining in close contact for a short time the chromosomes begin to separate from one another, and as they do so they cohere

at various points where their substance becomes drawn out to form anastomoses (fig. 5). Although it is possible that some of the anastomoses, which become very numerous in later stages, may originate after the manner of pseudopodia, it is clear that the earlier ones must be formed mainly by the coherence of the viscid substance of neighboring chromosomes originally in contact. Meanwhile the karyolymph has begun to form, the nuclear membrane differentiating where it comes in contact with the cytoplasm.

The telophasic alveolation or vacuolation of the chromosomes begins at about the time the latter begin to separate as above described. The vacuoles first appear within the chromosomes as somewhat obscure though rather sharply limited regions of circular or oval form (fig. 5). They develop not only along the axis of the chromosome but also near or against its periphery; in fact, an inspection of the figures shows that they may occur in almost every conceivable position and with no regular arrangement with respect to each other. At a slightly later stage they become clearer and more numerous (fig. 6).

This variety and irregularity in the arrangement of the vacuoles calls for special emphasis, because of the fact that the writers named in the first paragraph of this paper have interpreted the telophasic alveolation as a splitting, the chromosomes from this stage onward being consequently regarded as double. Attention is therefore directed to the conditions illustrated in figures 6–9. It is noticeable that the vacuoles may nearly all be along the margin of the chromosome (right edge of upper nucleus in figure 6), and also that two or three may lie side by side across the width of the chromosome (left edge of same nucleus). In figure 7 are shown two chromosomes in which the latter condition is especially pronounced: here it is manifestly impossible to speak of a split. Transverse sections of the chromosomes at these stages are particularly instructive (fig. 9). Such a section passing through a region where there is but one large vacuole more or less centrally placed has an appearance represented in figure 9*a*. A chromosome with a series of such central vacuoles would appear double if viewed from the side. This, however, is only a special case of a more general condition. Figures 9*b*-9*f* show sections passing through regions occupied by several vacuoles side by side, as in the chromosomes of figure 7 and those at the left in figure 6. It would seem to require no further argument to show that the chromosomes during these and the later telophase stages are not split ribbons or threads, but are irregularly alveolated cylinders; and that they can no more be called "double" than triple or quadruple.

The above described changes continue, gradually transforming the alveolated chromosomes with their anastomoses into a common reticulum. An examination of figures 10–13 will serve better than a written description to make clear the manner in which this transformation is accomplished. The whole nucleus enlarges, nucleoli appear, the anastomoses lengthen and

apparently become more numerous, and the alveolation of the chromosomes becomes more complete (fig. 10). The chromosomes at this time usually show a distinct polarity in their arrangement, as represented semidiagrammatically in figure 8. As the vacuoles within the chromosomes increase in size and number, their boundaries at the margin of the chromosome break down, allowing them to become continuous with the nuclear cavity. In this way the alveolar or vacuolate condition passes into a reticular one; each chromosome becomes an irregular netlike structure which is in no sense double. All of them together, with their connecting anastomoses, constitute the common reticulum of the late telophase and interphase or resting stages. The limits of the constituent chromosomes remain visible until a comparatively late stage (fig. 11).

Interphase and Rest. The degree to which the telophasic transformation is carried varies considerably in different nuclei, the amount of change being correlated with the rapidity with which the mitoses succeed one another. In the most active part of the root meristem it seems evident that the transformation may go no further than the stage represented in figure 11, the prophasic changes of the next mitosis setting in at once. In such an event the chromatin passes directly from the stage of figure 11 (telophase) to that of figure 14 (prophase): the anastomoses connecting the reticulate chromosomes begin to break down while the chromosomes are yet distinguishable, so that there is no time between the successive mitoses at which the limits of the chromosomes cannot be seen. It is plain that in such cases the structural identity of the chromosomes is not lost during the interphase.

The interphase condition most commonly found in the root meristem is that shown in figure 12. Here the telophasic transformation has been carried much further; the anastomoses for the most part cannot be distinguished from the other fine strands of the reticulate chromosomes, and the limits of the chromosomes cannot be made out with any certainty. Here and there are lighter regions which probably represent boundaries between the constituent chromosomes, and if the prophasic changes were to begin at this time the reticulum would almost surely break down along these lines. The chromatin may apparently continue in this state for some time, so it may properly be said to be in the "resting" condition.

In older tissue, but only rarely in the root meristem, the telophasic changes continue until the nucleus has the structure shown in figure 13. The chromosomes, all visible traces of whose limits have now been lost, form a common chromatic reticulum of very fine texture. Such a reticulum is ordinarily described as being made up of "granules of chromatin carried on a supporting network," and so it surely appears if not sharply stained or if viewed through lenses of insufficient resolving power. But careful examination, together with a comparison of the successive stages of the telophase, lead to a different interpretation. Since the structure of the

fine reticulum is the direct outgrowth of the progressive transformation shown in figures 5–12, it seems more probable that the "chromatin granules" are merely the heavier portions of the alveolated and reticulate chromosomes, and that the lighter "supporting network" consists simply of the thinner portions of the same together with the delicate anastomoses. As pointed out in the case of Vicia, the finer strands stain much less deeply than the coarser portions, so that one easily gains the impression of separate chromatin granules connected by delicate threads of another material. But in a tapering strand the color grows gradually deeper in passing from the thinner to the thicker portion, a fact which indicates that the reticulum consists of but a single substance, or, more probably, that the chromatin substance is very fluid in consistency and free to diffuse about within the other material which composes the framework, as suggested by Grégoire (1906). Although much evidence which has been brought forward by various workers indicates the presence of two principal and morphologically distinct elements in the nuclear reticulum, it is nevertheless probably true that the above interpretation will apply to many accounts describing autonomous chromatin units on a supporting achromatic network.

Prophase. As the prophasic changes begin, the reticulum becomes somewhat coarser and commences to break up into irregular band-like portions (fig. 14). As pointed out in the preceding section, the telophasic changes in rapidly multiplying cells may go no further than the stage represented in figure 11, where the limits of the chromosomes can easily be made out. If, now, such a nucleus should enter upon the prophase, there can be little doubt that it would be along the lines of chromosome union that the reticulum would break down, since along these lines are the delicate anastomoses, which would be the first to give way as the band-like portions begin to condense. A reticulum in which the telophasic transformation has been carried further, as in figure 12, also breaks down along its lighter zones. From what has been seen in the case of figure 11, it seems evident that these zones for the most part represent the interchromosomal spaces, so that here also argument may be made for the structural continuity of the individual chromosomes through the interphase or resting stage. In the case of a nucleus with such a fine and uniform reticulum as that of figure 13, it is manifestly impossible to determine by direct observation whether or not the lines of prophasic separation coincide with those of the preceding telophasic union. The evidence for the structural individuality of the chromosomes must here be indirect, and such indirect evidence is afforded by the many known instances in which the chromosomes in successive mitoses, although lost to view during the resting stages, not only remain constant in number but maintain constant differences in size and shape. Additional evidence is found in the fact that in cells dividing repeatedly in one plane, as in the root meristem, the separate bands or chromosomes appear in the prophase with the same orientation as that

shown by the chromosomes as they form the reticulum during the telophase (compare figs. 11 and 14).

The separating portions of the reticulum, each of them representing a chromosome, continue to condense, and the anastomoses between them become further broken down, so that they soon stand out with great distinctness (fig. 15). Since the early prophasic changes are in many respects simply the reverse of those occurring in the telophase, the structure of the chromosomes at these two stages is almost precisely the same. Vacuoles, or spaces enclosed during the condensation of the reticulum, may be found in all positions, median and peripheral, while large cavities open to the exterior on all sides. Transverse sections of chromosomes in this condition are shown in figure 16. It is perfectly evident that at this stage of the prophase, just as in the telophase, each chromosome is simply an irregular alveolar-reticulate cylinder, and has the form neither of a split thread or ribbon nor of a ladder-like structure characteristic of the incompletely split chromosomes of the later prophases. At the stage shown in figures 15 and 16 the chromosomes are in no sense double; the split marking the line of separation at the next metaphase has not yet appeared.

Each alveolar-reticulate chromosome now becomes transformed in a peculiar manner into a *single* (*i.e.*, not double) slender thread. Of all the morphological changes undergone by the chromosomes during mitosis this is one of the most difficult to observe and interpret. The staining must be particularly sharp to bring it out properly, and it is probable that it is passed through with considerable rapidity. These facts account in part for the absence of these stages from the descriptions of mitosis given by many investigators, and consequently for misinterpretations of the telophasic and early prophasic changes with respect to the splitting of the chromosomes. The transformation process, which is in progress in the nucleus shown in figure 17, is as follows.

As the chromatic material becomes increasingly condensed, the more slender strands, like the anastomoses at an earlier stage, and also the thinner walls bounding the peripherally situated enclosed spaces, become broken down, leaving the heavier portions of the chromosome in the form of a very irregular zigzag thread of uneven thickness. Various stages in this process are shown in figure 18. At the points marked *a* the dissolution of the finer portions can be seen occurring, and the reason for the crooked and lumpy appearance of the newly formed slender thread is apparent. In many cases the arrangement of the open spaces is such that the chromatic thread has a roughly spiral aspect, but in view of the relation it bears to the reticulate stages of the earlier prophases it can hardly be said to arise endogenously within the chromosome as some workers have maintained. The crooked thread at once begins to straighten out; this change in shape is associated with an equalization of the chromatic material, so that the thread gradually becomes more uniform in diameter. Here and there in the

heaviest portions a few small vacuoles may for a time persist, but for considerable distances the thread is completely without them.

The true split now develops in the slender threads. Almost as soon as a portion of a thread becomes sufficiently equalized a number of new openings appear, and it seems highly probable that they are the outgrowth of small vacuoles which are formed anew along the axis of the thread. Some of the openings elongate a little, making the thread clearly double for short distances (fig. 19); here for the first time a portion of a chromosome can be said to be truly double. It is a matter of extreme difficulty—indeed it is probably impossible—to tell certainly whether these small vacuoles and openings are all new prophasic developments or are in part retentions from the resting stage and hence from the preceding telophase. Soon after their formation the slender threads, so far as can be determined with the best optical equipment, are certainly single and devoid of vacuoles for long distances, whereas the vacuoles become very numerous later. After a comparison of many chromosomes in these stages the writer has concluded that in all probability a vacuole or open space is now and then retained from an earlier stage, but that the great majority of vacuoles and spaces which develop into a split in the slender thread are formed anew in the prophase.

As the vacuoles increase in number and enlarge into openings extending through the thread, the latter shortens and thickens, and takes the form of an irregular ladder-like structure (figs. 20, 21). A nucleus in this stage (fig. 22) has a superficial resemblance to one in the early prophase stages (fig. 15), and some writers have confused them, omitting the important stages which intervene. In figure 15 the chromosomes are in the form of irregular alveolar-reticulate cylinders, as shown by their cross section (fig. 16), whereas in figure 22 they exist as thread- or ribbon-like structures partially split by a series of median openings and are clearly double in cross section (see the free and cut ends in figures 21–23).

As already stated, Tradescantia appears to be less favorable for a study of the later prophases than Vicia. The open spaces in the chromosomes do not run together to form a continuous split so early as in the latter plant. The material of some of the cross pieces connecting the sides of the partially split threads gradually flows to the two sides where it accumulates in the form of paired lumps simulating divided granules as fully described in the account of Vicia. Many of them, however, remain unchanged until a very late stage, so that even after the threads have become much shortened and thickened to form the conspicuous heavy spirem stages some of them may show the openings not yet developed into a complete split (figs. 22, 23). In other chromosomes the splitting process has gone further, making them almost completely double (at right in figs. 22 and 23). In nuclei of these stages it is not difficult to discover several free ends which are not due to the microtome knife, so that certainly at this time, and probably at

earlier stages also, the chromosomes do not form a continuous spirem. On the other hand, it seems probable that some of the chromosomes may hang together end to end, since the number of ends which can be distinguished appears to be much smaller than the number which would be expected if all the chromosomes were free from one another.

The spindle now begins to differentiate in the cytoplasm, and the nuclear membrane contracts about the chromosomes. In the chromosomes the split now becomes complete, but as they continue to shorten and thicken their halves become so tightly pressed together that in many preparations they can scarcely be distinguished. As the contraction reaches its climax the nuclear membrane disappears (fig. 24), and the chromosomes, after loosening up as an irregular group, rapidly become arranged on the spindle with their halves clearly evident (fig. 1).

Discussion

A number of the features of somatic mitosis as the writer has found them have been compared with the results of other investigators in the paper on Vicia (1913) and need not be reconsidered here. In the present discussion attention will be limited to three important points: the time of chromosome splitting, the method of splitting, and the bearing of the results of this study on certain interpretations of the heterotypic prophase.

Time of chromosome splitting. Because of the exact manner in which the telophasic and prophasic changes are seen to occur when closely examined, the writer has contended that the definitive splitting of the chromosomes occurs in the prophase rather than in the telophase as several workers have urged. In the first place, the telophasic alveolation, as emphasized in the foregoing description, is a very irregular process, its result being the transformation of each chromosome into an irregular alveolar-reticulate structure showing nothing which can with any justice be called doubleness. After an inspection of the figures of longitudinal and cross sections of the telophase chromosomes (figs. 5–11) further argument on this point would seem to be superfluous. Secondly, the alveolar-reticulate bands into which the resting reticulum breaks down in early prophase, and which are probably in all cases continuous with the similar bands (chromosomes) of the preceding telophase, are not transformed directly into the split spirems of the later prophase, but give rise to single threads in which the definitive split is formed as the result of a process which appears to begin with the development of an axial series of new vacuoles. It has been shown that as these single threads are evolved most of the vacuoles and open spaces which had their origin in the preceding telophase, and which constitute the openings in the resting reticulum, become lost through the breaking down of their boundaries, so that the telophasic vacuoles, whether so situated as to make the chromosome double or not, take little or no part in the development of the definitive split.

It may here be questioned whether the vacuoles and open spaces which appear and split the thin prophasic thread may not be at least partly retentions from the preceding telophase, the split therefore being initiated in the telophase after all. This is a question which it has not been found possible to answer in many cases, since the changes in question occur in very minute structures which cannot be interpreted at all in any but the most favorable preparations. There can be no doubt, however, that the threads for considerable distances are actually single so far as the microscope will allow us to determine, and that many new vacuoles and open spaces develop where none were visible before. On the other hand it seems very probable that a few spaces of the earlier prophase, and hence of the preceding telophase, may occasionally persist in the heavier portions of the threads as they develop from the reticulate bands, such spaces if properly situated being incorporated in the later true split. But only in a very strained sense could such occasional vacuoles or spaces be said to constitute the initial stages of the split; their relation to it appears to be fortuitous rather than determinative.

It may also be questioned whether the single thread stage of the prophase, upon the importance of which the writer has insisted, is a phenomenon of general occurrence or is a special process peculiar to a few types of cells. To this question also no full answer can be given at present. It surely occurs in the root cells of Vicia and Tradescantia in spite of the fact that it does not appear in the descriptions given by other investigators of mitosis in these plants. It is also represented in Müller's (1911) figure 9 of *Najas marina*, and in the "spiral threads" figured by Bonnevie (1908, 1911, 1913) for Allium, Amphiuma, and Ascaris; by Wilson (1912) for certain insects; and by several other investigators. How much more widespread it may be cannot be stated, especially since the prophasic changes have been followed with sufficient care in so relatively few cases.

On the contrary, it is not impossible that in some forms the split spirem may develop directly from the alveolar-reticulate bands of the earlier prophase by a rearrangement of the vacuoles and openings to form a single median series as the structures become more slender, but the writer is not convinced that such a process has been demonstrated in any instance. Even if, for the sake of argument, it were assumed to occur, it would not necessarily follow that the telophasic vacuolation should be regarded as a splitting or that the chromosomes of the late telophase, resting stage and early prophase should be regarded as double when the vacuoles and openings have such an arrangement as that described for Vicia and Tradescantia. Chromosomes in this condition are not double in any sense of the word, even though they contain open spaces which may later join with others to form a split. The chromosome can be said to be "double" or "split" only when its substance has been separated into two distinguishable portions, either by the rearrangement of the vacuoles and spaces as provisionally

assumed, or, as is in all probability actually the case, by the formation of a median series of vacuoles and spaces which are for the most part if not entirely of prophasic origin. It may again be emphasized that in Tradescantia, as in Vicia, the alveolar-reticulate condition of the telophase and the early prophase does not pass directly into the split spirem stage as above provisionally assumed; but rather, by a peculiar process in which most if not all of the old vacuoles and openings are lost, the reticulate chromosome takes the form of a single thread in which the split then develops anew. In these forms the chromosome split, whether entirely new or partially built of vacuoles of earlier origin, cannot be regarded as anything but a prophasic development.

Method of chromosome splitting. Much interest centers about the exact manner in which the chromosomes undergo splitting because of its great importance in connection with current theories of the mechanism of heredity. The early view that the splitting of the chromosomes is primarily a division of a series of smaller units which it contains has been widely accepted, especially by those whose investigations have been concerned with the cytological aspects of the problem of inheritance. The hypothesis which postulates the existence of small units of inheritance, or genes, within the chromosomes has been of incalculable value in organizing the data of genetics, and new evidence constantly adds to the probability that such units are not purely conceptual ones. But it must be said that this evidence is genetical rather than cytological in nature. Although many cytologists have regarded the visible chromatin accumulations or granules as such units and have figured their division, others have found it increasingly difficult to see in these chromomeres anything significant in this connection. For the most part they seem to be quite inconstant in number and disappointingly irregular in behavior.

In the somatic cells of Tradescantia, as in Vicia, chromosome splitting seems to be initiated by a series of axial vacuoles which quickly develop into openings through the homogeneous chromatin thread, and not by the division of chromatic granules supported by the thread. As the openings become more numerous the chromosome takes the form of a ladder, the rounds being represented by the material between the successive openings (fig. 21). As the rounds or cross pieces gradually become thinner and finally break at the middle, thus completing the split, their material accumulates in two small lumps opposite each other in the two halves of the chromosome. The "paired granules" or "divided granules" described by many workers are without doubt to be explained in this manner. Such being their mode of origin, it is difficult to assign to them the rank of morphological units, or to attribute to them any specialized function in the hereditary process. In the microsporocytes of Vicia, however, the writer has observed chromatic granules of a much more definite character, but is not prepared to make any statement with regard to their significance.

The view that such granules do have some special significance is strongly favored by Wenrich's (1916) striking observations on Phrynotettix. Not only do the granules or chromomeres of a given member of the chromosome group in this form have relatively constant sizes and positions, but they also show close correspondence in the two members of a conjugating homologous pair. This is precisely the type of chromosome organization called for by our most promising theory of the cytological mechanism of heredity, which it is hoped will find further verification in additional observations as carefully made as those of Wenrich.

Bearing on problem of chromosome reduction. As stated in the introduction, the theory of telophasic splitting has been incorporated in an interpretation placed upon the reduction phenomena by Fraser (1914), Digby (1914, 1919), Nothnagel (1916), and certain other writers. The split seen in the early heterotypic prophase is said to have its origin in the telophase of the last premeiotic division, each chromosome persisting through the intervening resting stage in the double condition. It is consequently held, as fully stated by Digby (1919) in her account of the archesporial and meiotic phases in Osmunda, that the lateral pairing of slender threads in the heterotypic prophase, which a large school of cytologists has regarded as a conjugation of entire chromosomes, is in reality only the reassociation of the two halves of one chromosome which has been split in the preceding telophase. Such a reassociation is thought to occur in every prophase, somatic and meiotic, since these workers regard chromosome splitting as universally a telophasic phenomenon. The split thus thought to form in the premeiotic telophase functions in the homoeotypic mitosis; the latter mitosis is therefore looked upon as a continuation of the premeiotic division, the heterotypic mitosis being an interpolated process bringing about reduction. Not only does this premeiotic split reappear in the anaphase of the heterotypic mitosis to function in the homoeotypic, but a new split developing in the heterotypic telophase, after being temporarily obscured, functions in the post-homoeotypic division.

As the writer (1920) has pointed out in a review of Digby's contribution, the above outlined theory of reduction has certain advantages, for "it allows one interpretation to be placed upon the double spirem in both somatic and heteroptyic prophases, . . . and it also helps to explain the sudden appearance of the split for the second maturation mitosis in the anaphase of the first."

But can it be said that the chromosomes undergo splitting in the last premeiotic telophase and remain double through the ensuing resting stage? The writer believes that it has been shown in the case of ordinary somatic mitosis in Vicia and Tradescantia that the telophasic alveolation is in no sense a split. This conclusion rests upon the facts brought out in a detailed analysis of the telophasic changes themselves, and upon the fact that the early prophasic reticulate condition, which all grant is continuous with

that of the preceding telophase, does not pass directly into the double spirems, but gives rise to single threads in which a new split develops, entirely or mainly by a new vacuolation, making the threads really double for the first time. This being true, it follows that the chromosomes at the beginning of the heterotypic prophase are *single* (although alveolar-reticulate), unless, indeed, the premeiotic telophase differs fundamentally from other somatic telophases, which is not supposed to be the case. Consequently, if it is argued that the doubleness of the spirem in the heterotypic prophase is due to a splitting and not to a conjugation, it must be done upon other grounds; the principle of the telophasic split is evidently a false premise.

From the above considerations it appears that chromosome behavior during the somatic telophase, instead of giving the key to the reduction process, shows rather that the solution of this perplexing problem must be reached mainly through a more refined analysis of those changes in the heterotypic prophase itself which have led so many observers to conclude that the association of chromatic threads at that stage represents the conjugation of entire chromosomes which separate at the first maturation mitosis.

Summary

The principal results of the present study of Tradescantia may be summarized as follows:

1. During telophase the chromosomes become transformed by a process of irregular vacuolation into alveolar-reticulate structures which together make up the resting reticulum. In rapidly multiplying cells the visible limits of the constituent chromosomes may not be entirely lost between successive mitoses.

2. In prophase the constituent reticulate chromosomes separate from one another through the breaking down of their connecting anastomoses; each gives rise to a single slender chromatic thread in which the definitive split develops as a new formation, though old vacuoles may occasionally be incorporated in it.

3. The telophasic vacuolation cannot be interpreted as a splitting of the chromosomes; the chromosomes are therefore not double during the resting stages. The splitting of the chromosomes is a phenomenon of the prophase.

4. No direct evidence has been found favoring the view that the splitting of the chromosomes is primarily a division of smaller chromatic units or chromomeres.

5. Interpretations of the phenomena of the heterotypic prophase are unsound in so far as they rest upon the assumption of telophasic splitting in somatic cells.

Cornell University

LITERATURE CITED

Bonnevie, K. 1908. Chromosomenstudien. I. Chromosomen von Ascaris, Allium und Amphiuma. Arch. Zellforsch. 1: 450–514. pls. 11–15. figs. 2.

——. 1911. Chromosomenstudien. III. Chromatinreifung in *Allium cepa* [illegible]. Arch. Zellforsch. 6: 190–253. pls. 10–13.

——. 1913. Ueber die Struktur und Genese der Ascarischromosomen. Arch. Zellforsch. 9: 433–457. figs. 7.

Digby, L. 1910. The somatic, premeiotic, and meiotic nuclear divisions of *Galtonia candicans*. Annals of Botany 24: 727–757. pls. 59–63.

——. 1914. A critical study of the cytology of *Crepis virens*. Arch. Zellforsch. 12 97–146. pls. 8–10.

——. 1919. On the archesporial and meiotic mitoses of Osmunda. Annals of Botany 33: 135–172. pls. 8–12. 1 fig.

Farmer, J. B., and Shove, D. 1905. On the structure and development of the somatic and heterotype chromosomes of *Tradescantia virginica*. Quart. Journ. Micr. Sci. 48: 559–569. pls. 42, 43.

Fraser, H. C. I., and Snell, J. 1911. The vegetative divisions in *Vicia Faba*. Annals of Botany 25: 845–855. pls. 62, 63.

Fraser, H. C. I. 1914. The behavior of the chromatin in the meiotic divisions of *Vicia Faba*. Annals of Botany 28: 633–642. pls. 43, 44.

Grégoire, V. 1906. La structure de l'élément chromosomique au repos et en division dans les cellules végétales (Racines d'Allium). La Cellule 23: 311–353. pls. 1, 2.

Lundegårdh, H. 1910. Über Kernteilung in den Wurzelspitzen von *Allium cepa* und *Vicia Faba*. Svensk. Bot. Tidskr. 4: 174–196. figs. 11.

——. 1912. Das Caryotin im Ruhekern und sein Verhalten bei der Bildung und Auflösung der Chromosomen. Arch. Zellforsch. 9: 205–330. pls. 17–19. figs. 9.

Miyake, K. 1905. Über Reduktionsteilung in den Pollenmutterzellen einiger Monokotylen. Jahrb. Wiss. Bot. 42: 83–120. pls. 3–5.

Müller, H. A. C. 1913. Kernstudien an Pflanzen. I und II. Arch. Zellforsch. 8: 1–51. pls. 1, 2.

Nothnagel, M. 1916. Reduction divisions in the pollen mother cells of *Allium tricoccum*. Bot. Gaz. 61: 453–476. pls. 28–30. 1 fig.

Sharp, L. W. 1913. Somatic chromosomes in Vicia. La Cellule 29: 207–331. 2 pls.

——. 1920. Mitosis in Osmunda (Review). Bot. Gaz. 69: 88–91.

Strasburger, E. 1900. Ueber Reduktionsteilung, Spindelbildung, Centrosomen und Cilienbilder im Pflanzenreich. Hist. Beitr. 6. 224 pp. 4 pls. Jena.

Wenrich, D. H. 1916. The spermatogenesis of *Phrynotettix magnus* with special reference to synapsis and the individuality of the chromosomes. Bull. Mus. Comp. Zool. Harvard Coll. 60.

Wilson, E. B. 1912. Studies on chromosomes. VIII. Observations on the maturation-phenomena in certain Hemiptera and other forms, with considerations on synapsis and reduction. Journ. Exp. Zool. 13: 345–449. 9 pls.

EXPLANATION OF PLATES

PLATE XXII

All figures except no. 8 were drawn at the level of the table with the aid of an Abbé camera lucida under a Zeiss apochromatic objective, 2 mm. N.A. 1.40, with compensating ocular 18. They have been reduced one-half in reproduction and now show a magnification of 1900 diameters. Fig. 8, × 950.

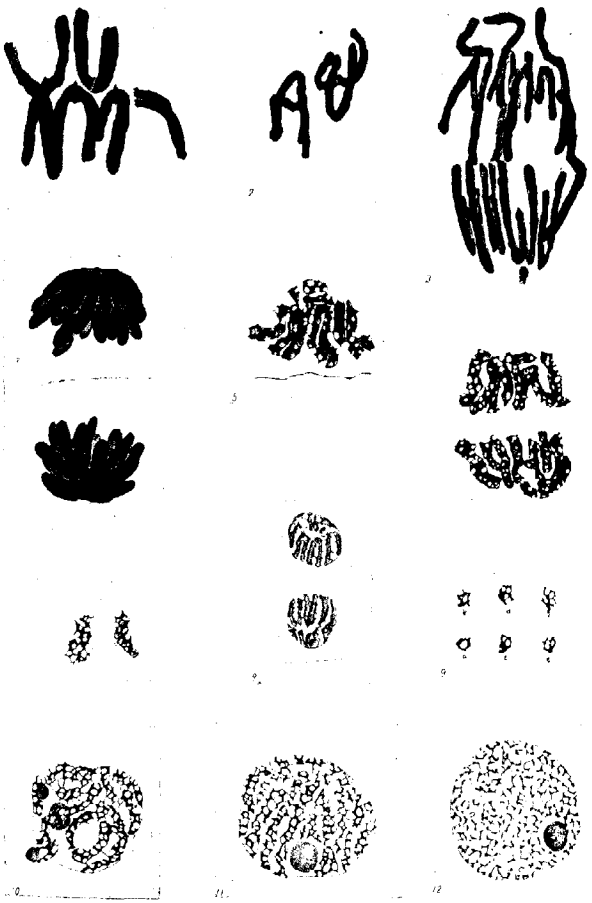
FIG. 1. Metaphase: chromosomes attached to spindle by middle points.

FIG. 2. Anaphase: daughter chromosomes separating.

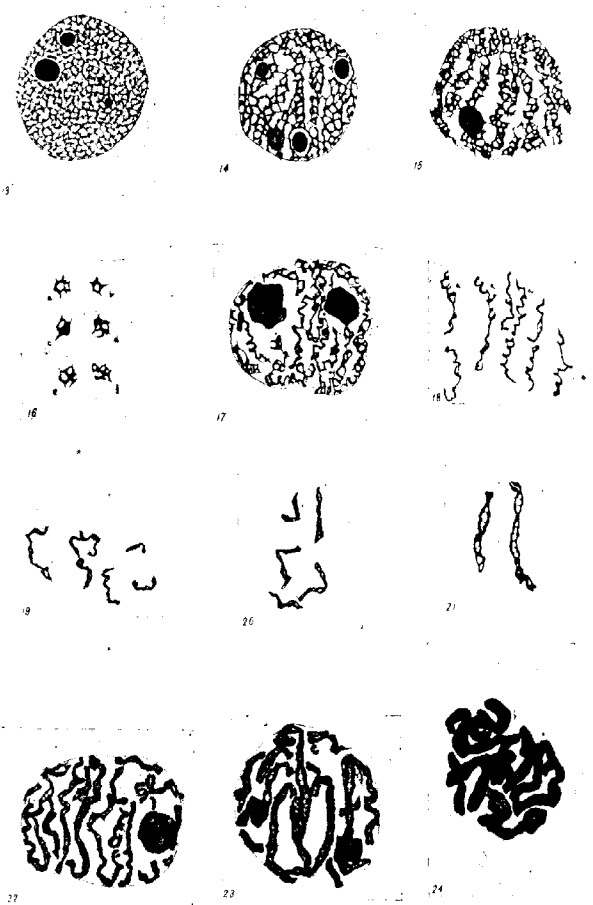
FIG. 3. Later stage: daughter chromosomes passing to poles.
FIG. 4. Late anaphase: chromosomes massing at poles.
FIG. 5. Telophase: vacuoles appearing within chromosomes; anastomoses present.
FIG. 6. Slightly later stage; note arrangement of vacuoles.
FIG. 7. Two telophase chromosomes, showing irregularity of vacuolation.
FIG. 8. Telophase, showing polarized arrangement of chromosomes (camera lucida sketch).
FIG. 9. Cross sections of telophase chromosomes, showing the same.
FIG. 10. Later telophase: nucleus larger and nucleoli present.
FIG. 11. Late telophase: limits of chromosomes still visible.
FIG. 12. Interphase or resting stage.

PLATE XXIII

FIG. 13. Resting stage in which telophasic changes have gone further.
FIG. 14. Early prophase: reticulum breaking up into constituent chromosomes.
FIG. 15. Later stage: chromosomes further separated and more condensed.
FIG. 16. Cross sections of chromosomes like those of figure 15.
FIG. 17. Prophase nucleus with most of its chromosomes in single thread stage.
FIG. 18. Chromosomes in single thread stage; development of this condition from reticulate stage shown at *a*.
FIG. 19. Splitting of single threads.
FIGS. 20, 21. Later stages: vacuoles and openings more numerous; chromosomes thicker.
FIG. 22. Prophase nucleus with some chromosomes partially and some completely split.
FIG. 23. Later stage: chromosomes heavier but not completely split.
FIG. 24. Late prophase: chromosomes swollen and split obscured; nuclear membrane has disappeared and spindle is developing.



SHARP: SOMATIC CHROMOSOMES IN TRADESCANTIA.



SHARP: SOMATIC CHROMOSOMES IN TRADESCANTIA.